

# BOTANISK TIDSSKRIFT

51 - 52

*Udgivet af*

DANSK BOTANISK FORENING

—  
51. BIND



KØBENHAVN

EJNAR MUNKSGAARDS FORLAG

1954

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1954

ANDELSBOGTRYKKERIET I ODENSE







## The Danish Species of *Geoglossum* and Related Genera

By ERIK BILLE-HANSEN

The genus *Geoglossum* sensu PERSOON has not interested Danish botanists very much. THEODOR HOLMSKJOLD depicted 3 species in his wonderful book "Beata ruris otia fungis danicis impensa." He described *Clavaria mitrata* (= *Corynetes atropurpurea*), *Clavaria mitrata* var. *viridis* (= *Microglossum viride*), and *Clavaria ophioglossoides* (= *Trichoglossum* sp.). The descriptions and plates were made between 1762 and 1767 but not published until 1790. C. F. SCHUMACHER (1803) mentioned "*Geoglossum glabrum*" and "*Geoglossum viride*". E. ROSTRUP (1892) described two new species, viz. *Microglossum arenarium* (= *Corynetes arenarius* (ROSTR.) DUR.) and *Leptoglossum littorale* (= *Geoglossum littorale* (ROSTR.) NANNF.). Finally J. LIND (1913) gave a survey of what was found of *Geoglossa* in the herbarium of E. ROSTRUP and others. He just recorded the names but did not try to revise the material.

On this basis the author found it desirable to take up a study of the *Geoglossa* and has for some time made collections of the various species. The present paper gives an account of these collections, of numerous collections sent to me by colleagues, and of the older specimens in Danish herbaria. Records in literature, not substantiated by specimens, are largely disregarded. The older literature is of no value as names as "*Geoglossum glabrum*" or "*Trichoglossum hirsutum*" have been used in a very broad and ill defined sense. In my revision I have mostly used the monographs of ELIAS J. DURAND (1908 and 1921) and J. A. NANNFELDT (1942) to which papers I refer for the synonymy of the various species.

The *Geoglossa* are probably saprophytes which are often found in moist stations (wet woods, meadows, slopes of ravines or ditches) but also met on more dry localities. The lawns on which *Hygrophorus* spp., *Clavaria corniculata*, and *C. luteo-alba* are common are generally

good localities for f. inst. *Geoglossum fallax*, *glutinosum*, *nigritum*, *starbaeckii* and others. The dark species are very much alike macroscopically and as they often grow together, it is necessary to collect with great care. It is possible to sort out the different species with the aid of a pocket lens but the microscope is indispensable for the correct determination. A section of the hymenium and the stem shows all necessary details. A gentle pressure on the coverslip will separate the paraphyses and place the spores side by side in the ascus. Dried material is preferable to specimens preserved in alcohol. If the paraphyses in dried material are difficult to see, a drop of 1% KOH may make them swell and be discernible.

Abbreviations: Specimens from the Botanical Museum of the University of Copenhagen are marked with "B.H.", those from the herbarium of the Dept. of Plant Pathology of the Royal Agricultural College marked with "P.H."

#### General diagnosis:

Ascomata fleshy, erect, stipitate, clavate, hymenium covering only the upper portion; asci clavate-cylindrical, opening by a pore; spores 4-8, cylindrical or clavate-cylindrical, 0-15 septate; paraphyses numerous, septate, in most species confined to the ascigerous portion.

#### Key to the genera.

- A. Ascomata bright colored ..... 1. *Microglossum*
- A. Ascomata black or blackish
  - B. Spores hyaline ..... 2. *Corynetes*
  - B. Spores fuliginous or brown
    - C. Hymenium without spines or setae ..... 3. *Geoglossum*
    - C. Hymenium with black, thickwalled cystidia ..... 4. *Trichoglossum*

To this four genera DURAND (1908) added a fifth one, *Gloeoglossum*, in which he placed the viscid species of *Geoglossum* which have the whole stem covered with a continuous layer of paraphyses. This genus has not been accepted by other mycologists. C. G. LLOYD (1916) preferred the classical delimitation of *Geoglossum*, finding the distinguishing characters of the different genera too vague. I have been tempted to follow LLOYD but in this survey I prefer to use the classification outlined in the key.

#### 1. *Microglossum* GILL.

Bright colored ascomata. Spores hyaline, multiseptated at maturity. I have not seen any septated spore in my material but very often multi-guttulate ones. The two scandinavian species may be distinguished as follows. (Vide IMAI (1938)):

1. Stem smooth, glossy, fibrous, olivaceous epithecium . . . . . *M. olivaceum*
2. Stem furfuraceous, squamulose, scarcely fibrous, green epithecium *M. viride*

*Microglossum olivaceum* (PERS. ex FR.) GILL.

Ascigerous portion (according to IMAI (1938)) madder brown then deep-olive, finally light-danube green. Stem walnut-brown above and lighter below, then cinnamon to tawny-olive, then through dark greenish glaucous to dark american green. Spores:  $11-18\mu \times 4-6\mu$  (I found  $14-17\mu \times 3.5-4\mu$ ).

Jylland: Lindberg at Randers, common between various *Clavariae* 1.9.1946, A. B. KLINGE. Karmark at Randers, 9.9.1946, A. B. KLINGE. Sjælland: Common at Køge Strandskov, 3.11.1942, M. P. CHRISTIANSEN. Frederikslund Skov, 2.10.1953, M. LANGE.

*Microglossum viride* (PERS. ex FR.) GILL.

Ascigerous portion dark olive-green, stem furfuraceous-squamulose, pale pea-green. Spores  $17-21 \times 3.5-4.5\mu$ . (IMAI:  $14-22 \times 5-6\mu$ ).

Jylland: Houlbjerg Skov (*Quercus* and *Fagus*) at Laurbjerg, 6.9.1953, A. B. KLINGE. Als Nørreskov (*Fagus*) 15.10.1950, N. F. BUCHWALD. Sønderballe Skov, 4.9.1954, Å. GRABAU. Moesgård Skov, 25.9.54. K. TEILMANN. Sjælland: Boserup Skov, 24.9.1927, F. H. MØLLER (P. H.) and 26.9.1927, M. P. CHRISTIANSEN. Jægersborg Dyrehave, Sept. 1881, V. SARAUW. Ibid. 10.10.1943, N. F. BUCHWALD (P. H.). Lyngby Mose, HOFFMEYER. Strandmøllen, INGER WARMING. Gandløse Ore, 10.9.1916, C. FERDINANDSEN (B. H.). Ravnsholt Hegn, 2.10.1927, J. GRØNTVED (B. H.). Hornbæk under *Quercus*, B. BOOTS. Gribskov, 18.9.1953, E. BILLE-HANSEN.

## 2. *Corynetes* HAZSL.

Dark brown to black species. Spores hyaline, 3-multiseptate. I have also here only seen multiguttulate spores.

1. Paraphyses hyaline, apically conglutinated by amorphous matter into a conspicuous vinaceous brown epithecium . 1. *C. atropurpureus*
2. Paraphyses conspicuously brown . . . . . 2. *C. arenarius*  
(Vide also *Geoglossum littorale* (ROSTR.) NANNFELDT.)

1. *Corynetes atropurpureus* (BATCH ex FR.) DUR.

Plants sometimes slender, sometimes rather irregular wrinkled and twisted. Dark to black with a faint tint of purplish brown. Spores  $25-30 \times 3-4\mu$ .

Jylland: Guddal at Gerum, 22.8.1950, TYGE CHRISTENSEN. Near the mouth of Tversted Å, 16.5.1952, A. B. KLINGE. At Stampen Mølle near Århus, at the edge of old molehills, autumn 1767, THEODOR HOLMSKJOLD. Sjælland: Common at Mogenstrup Ås, 9.10.1927, M. P. CHRISTIANSEN. Jægersborg Dyrehave, 11.10.1953, M. P. CHRISTIANSEN.

## 2. *Corynetes arenarius* (ROSTR.) DUR.

Only in sand dunes but not always near the sea. (Vide ANDERSSON 1950). Irregular contorted, often lobed, with a mycelia sand bag at the base of the stem.

Jylland: Vendsyssel, Gårdbogård, 2.8. and 17.8.1890, E. and O. ROSTRUP (B. H.). Skagen, 2.10.1902, M. KRØYER (P. H.). Between Kandestederne and Bunken, 5.9.1929, M. HYLANDER (ANDERSSON 1950). Råbjerg Mile, 5.9.1929, K. WINSTEDT. Same locality 1950, K. TOFT, M. LANGE. Svinkløv, 1.10.1918, C. H. OSTENFELDT (B. H.). Borris, 1908, Ø. WINGE, (B. H.). Dunes west of Nyminde Plantage, 1.9.1954, R. HEIM. Sjælland: Hornbæk, 7.10.1893, E. ROSTRUP, (B. H.). Tisvilde Hegn, 5.10.1954, M. LANGE. Bornholm: Due Odde, 18.10.1954, M. LANGE.

## 3. *Geoglossum* PERS. ex FR.

Brownish black to black ascomata, spores fuliginous, septated. Paraphyses numerous, septate, hyaline or brownish. In some species as for instance *G. nigritum* the spores ripen simultaneously or nearly so, having all practically the same colour and no variation in number of septa, but in others (as for instance *G. fallax*) the same section shows spores varying from hyaline to brown, with 0–11 septa. NANNFELDT used this two types in his subdivision of the genus. I use his key but have changed it somewhat here and there. Species not found in Denmark are placed in brackets.

### Group 1.

Viscid when fresh. Paraphyses not confined to the hymenium but continuing down to base of stem.<sup>1)</sup>

#### A. Spores 0–7 septate when mature

- a. Spores 0–7 septate, often only 3-septate, 55–110  $\mu$  long. . . 1. *G. glutinosum*
- b. Spores 7-septate, 43–65  $\mu$  long. . . . . (*G. affine* (DUR.) LLOYD U.S.A.))

#### B. Spores 15-septate when mature . . . . . 2. *G. peckianum*

### Group 2–5.

Not viscid when fresh. Paraphyses confined to the hymenium.

### Group 2.

Spores at maturity normally 15-septate. Asci 8-spored.

- a. Spores early and almost simultaneous taking the brown colour. Paraphyses not agglutinating.
  - x. Spores 120–180  $\mu$  long. Paraphyses terminating in 1–3 pyriform or ellipsoidal cells, constricted at the septa. . . . . (*G. pygmaeum* GER. ex DUR. (U.S.A., Java))
  - xx. Spores (104–)110–115(–125)  $\mu$  long. Paraphyses remotely septate. . . . . (*G. pumilum* WINT. (Brazil, Bermuda, Virginia, Japan))

<sup>1)</sup> The paraphyses of dried specimens swell appreciably in KOH and have a characteristic translucent appearance (narrow hyphae with gelatinous walls).



- b. Spores hyaline until very late, 60–95  $\mu$ . The straight paraphyses agglutinated into a brown epithecium. (*G. alveolatum* (DUR. ex REHM) DUR. (U.S.A., Japan))

### Group 3.

Spores only tardily coloured and septated, number of septa very variable, generally less than 15, but more than 7. Asci 8-spored but spores often of very different sizes.

- A. Spores gracile, clavate-cylindrical, distinctly narrow towards the ends, especially towards the lower one.
- Paraphyses hyaline or faintly coloured, strongly adherent and interspersed with  $\pm$  copious amorphous brown matter, sparingly septate, often somewhat constricted at the septa, strongly curved or circinate above,  $\pm$  abruptly dilated (to 10  $\mu$ ) apically. Spores as a rule 80–100  $\mu$  long 3. *G. fallax*
  - Paraphyses distinctly coloured, very numerous and slender, discrete, though interspersed with scanty brown matter, remotely septate, curved, not or only slightly constricted at the septa (in shape strongly resembling those of *Corynetes arenarius*). Spores as a rule 65–85  $\mu$  long. 4. *G. starbaeckii*
- B. Spores short and stout, almost cylindrical with rounded ends, 55–75  $\mu$  long. Paraphyses (nearly) hyaline, straight, with pyriform or globose apices, agglutinated into a conspicuous brown epithecium . . . . . (*G. intermedium* DUR. (North America))

### Group 4.

Spores early and almost simultaneously coloured and 7-septated, distinctly clavate.

- A. Paraphyses not adherent, remotely septate, strongly curved.
- Asci 4–6-spored . . . . . (*G. montanum* NANNF. (Sweden))
  - Asci 8-spored
    - Paraphyses only slightly dilated apically, not constricted at the septa. . . . . 5. *G. nigrum*
    - Spores much longer than the asci, cells barrelshaped or united into barrel-shaped pairs with constrictions between the pairs 6. *G. simile*
- B. Paraphyses brown, straight and adherent in clusters.
- The cells of the paraphyses rapidly increasing in size towards the tips reaching a diameter of 10–15  $\mu$ . Stem gracile. Sphagnophilous. 7. *G. glabrum*
  - Paraphyses not or only slightly increasing towards the tips, apical cell not exceeding 8  $\mu$  in breadth. Mostly sand-inhabiting, the whole fruitbody strongly compressed . . . . . 8. *G. cookeianum*

### Group 5.

Spores only tardily coloured and septated, at maturity with 7 or fewer septa. Asci 8-spored. Paraphyses  $\pm$  agglutinated by amorphous brown matter. (Obs. Care must be taken not to confuse this group with depauperate or juvenile fruitbodies of species belonging to group 3 or 4.)

- A. Paraphyses strongly coloured (as dark as in *Corynetes arenarius*) and strongly adherent. Spores pale brown . . . . . 9. *G. littorale*
- B. Paraphyses hyaline or subhyaline, apically very irregularly dilated, straight or curved, somewhat resembling those of *G. fallax*. . . . . (*G. elongatum* STARB. ex NANNF. (Sweden))

- C. Paraphyses stout, distinctly coloured, straight, apically globose or pyriform..... (*G. vleugelianum*  
NANNF. (Sweden))

1. *Geoglossum glutinosum* PERS. ex. FR.

Distribution: Europa, North America, and Asia (Japan).

The contrast between the dark brown, viscid stem and the dull, black club makes this species easy to recognise in the field. The two other viscid species *G. affine* and *G. peckianum* are according to DURAND uniformly black when fresh. When dry the stem darkens and makes characteristically longitudinal furrows. It often throws many grayish brown spores with only one septum.

Jylland: Viborg Nørresø, 1.11.1903, J. LIND. Ry, Knudsø, between grass on meadow, N. F. BUCHWALD. Djursland. Rygård, on common, 25.10.1953, A. B. KLINGE. Djursland, Glatved chalk hills, 27.10.1953, A. B. KLINGE. Mariager, Dyrby Krat, grass field with *Juniperus*, 27.11.1953, A. B. KLINGE. Læsten Bakker at Randers, 8.11.1953, A. B. KLINGE. Fyn: Klingstrup Skov, 8.10.1873, E. ROSTRUP (B. H.). Sjælland: Solrød Strand, 14.10. and 16.10.1927, M. P. CHRISTIANSEN. Common at Køge, 8.11.1942, M. P. CHRISTIANSEN. Tisvildeleje, open grass field, 31.10.1953, M. LANGE. Vaserne at Holte (common), 11.10., 1.11. and 6.11.1953, E. BILLE-HANSEN and M. LANGE. Jægersborg Dyrehave, various meadows, 11.10., 17.10. and 15.11.1953, E. BILLE-HANSEN and M. LANGE.

2. *Geoglossum peckianum* CKE.

Distribution: North America Asia (Japan), Europa (England, France, Sweden, Denmark).

New to Denmark. Rather common in U.S.A. The 15-septated spores and the strongly coiled and twisted paraphyses makes this viscid species easy to recognise.

Jylland: Lindet Krat by Arild, 2.9.1954, M. LANGE. Sjælland: Geels Skov, 23.9.1888, OVE ROSTRUP. (B. H. as *G. ophioglossoides*, 7 plants.)

3. *Geoglossum fallax* DUR.

Distribution: North America, Europe and Asia (Japan).

This is the most common *Geoglossum* in Denmark. The fruit bodies are dark brown, almost black specimens are not rare. Like NANNFELDT I have seen that *G. fallax* varies continuously from types with hyaline paraphyses which are strongly adherent and very difficult to observe owing to the big amount of amorphous matter—to types with faintly coloured, easily discernible paraphyses with only trace of amorphous substance.

Jylland: Fladbro near Randers. Shortgrassed meadow between a hill and Nørreå, 5.11.1953, A. B. KLINGE. Dyrby Krat at Mariager, 22.11.1953, A. B.

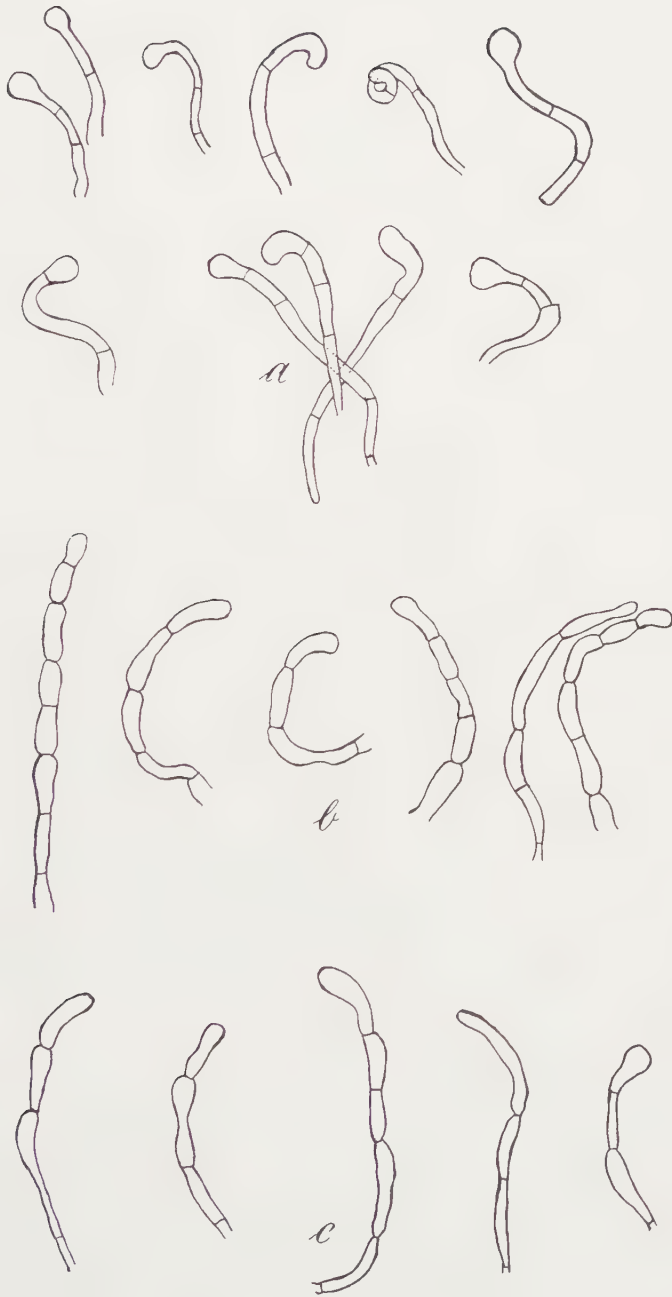


Fig. 1: a. *Geoglossum fallax*: 11 paraphyses. b. *G. starbaeckii*: 6 paraphyses. c. *G. nigrum*: 5 paraphyses.

KLINGE. Viborg Nørresø, 1.11.1903 (mixed with *G. glutinosum*), J. LIND, (B. H.). Nørager Have, 16.10.1878, E. ROSTRUP, (B. H.). Fyn: Klingstrup Skov, 8.10.1873, E. ROSTRUP, (B. H.). Sjælland: Solrød Strand, between grass, 16.10.1927, M. P. CHRISTIANSEN. Common at Køge, 4.11. and 19.11.1942, M. P. CHRISTIANSEN. Jægersborg Dyrehave, 7.11.1943, M. P. CHRISTIANSEN and J. P. JENSEN, Kongelunden october 1948, E. BILLE-HANSEN and M. LANGE. Jægersborg Dyrehave, the "*Larix*"-meadow, 21.10.1948. Jægersborg Dyrehave, meadow at Skovridergården, 11.10.1953, the mycological congress (4 collections). Same locality, 17.10.1953, E. BILLE-HANSEN and 23.10.1953, M. LANGE. Vaserne, meadows near Holte, M. LANGE (4 collections). Same locality 6.11.1953, E. BILLE-HANSEN and M. LANGE (5 collections). Stensholts Indelukke south at Gribskov, on a hill, 8.11.1953, M. LANGE (5 collections). Picea plantation in Gribskov, 8.11.1953, M. LANGE. Jægersborg Dyrehave, on sandy hills, 15.11.1953, E. BILLE-HANSEN (4 collections). Strøby Strand, "*Soløje*", "*Hygrophorus*" meadow, 22.11.1953, E. BILLE-HANSEN. Frederikslund Skov, 26.12.1953, M. LANGE.

#### 4. *Geoglossum starbaeckii* NANNF.

Distribution: Europe (Norway, Sweden, Denmark).

This species grows on the same localities as *G. fallax* and varies like that in colour from brown to nearly black. The two species may often be distinguished in the field by means of the scales. They are more coarse and flaky in *G. fallax* while finer and regularly arranged looking like the surface of a rasp in *G. starbaeckii*. The best and most constant character is the paraphyses, which in *G. starbaeckii* are distinctly brown, slender, never agglutinated resembling those of *Corynetes arenarius*.

Jylland: Læsø, 6.6.1897, C. H. OSTENFELD (B. H.). Tarm, in pasture 22.10.1944, K. BÜLOW (P. H.). Læsten Bakker at Randers, grassy slopes with *Calluna* and *Empetrum*, 8.11.1953, A. B. KLINGE, (3 collections). Ajstrup at Hadsund, 31.5.1953, A. B. KLINGE, (P. H.). Fyn: Klingstrup Skov, 8.10.1873, E. ROSTRUP, (B. H.). Låland: Billitze, 1.7.1922, C. H. OSTENFELD. Sjælland: Køge, on common, 3.11.1943, M. P. CHRISTIANSEN. Stenholts Indelukke near Gribskov, 8.11.1953, M. LANGE (3 collections).

#### 5. *Geoglossum nigrum* CKE.

Distribution: Europe, North America, and Asia (Japan).

Spores  $54-85 \times 6 \mu$ . Paraphyses faintly brown, not constricted but often somewhat swollen below the septa.

Jylland: Ry, Knudsø, between grass on meadow, 10.10.1951, N. F. BUCHWALD, (P. H.). Sønderballe Skov, 4.9.1954, Å. GRABAU. Fyn: Between grass on a road at Kværndrup, 24.9.1866, E. ROSTRUP, (B. H.). Between grass on a road at Skårup, 5.10.1873, E. ROSTRUP, (B. H.). Sjælland: Vallø Dyrehave, 20.10.1943, M. P. CHRISTIANSEN. Vaserne near Holte, pastures, 1.11.1953, M. LANGE. Jægersborg Dyrehave, "Skovriderengen", 17.10.1953, E. BILLE-HANSEN.



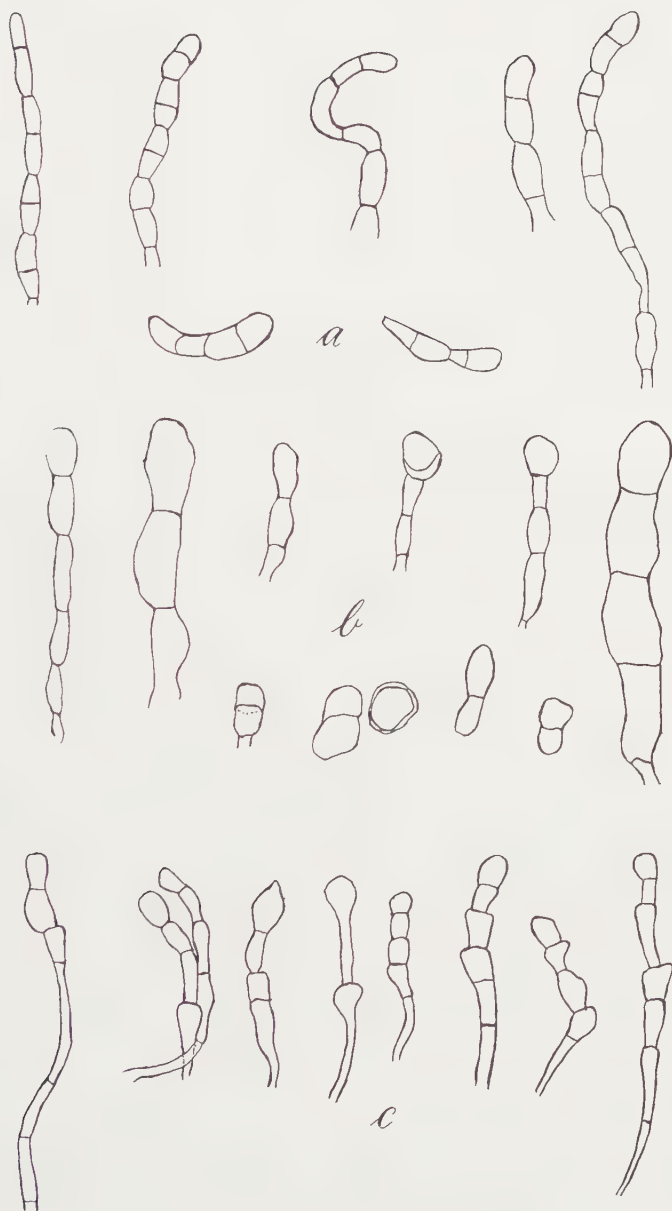


Fig. 2: a. *Geoglossum simile*: 5 paraphyses and 2 fragments. b. *G. glabrum*: 6 paraphyses and 5 fragments. c. *G. cookeianum*: 9 paraphyses.

6. *Geoglossum simile* PECK.

Distribution: North America, Asia (Japan), Europe (Denmark).

This species, which is new to the European flora, is easily recognised by its peculiar paraphyses. They are faintly coloured, not adherent. Their cells are barrel-shaped, mostly united in barrel-shaped pairs with constrictions only between the pairs. The paraphyses often break into pieces at the constriction. The fragments look like conidial chains of *Bispora*. *G. nigrum* has no constricted paraphyses and *G. cookeianum* and *G. glabrum* have both distinctly coloured, adherent paraphyses.

Sjælland: Rude Skov, 28.8.1887, S. RÜTZOU as *G. glabrum*, one specimen in formalin, (B. H.).

7. *Geoglossum glabrum* PERS. ex FR., emend. CKE.

Distribution: Europe and Asia (Japan).

NANNFELDT has shown that *Geoglossum glabrum* sensu DURAND comprises 3 species viz. *G. glabrum* PERS. ex FR., emend. CKE., *G. simile* PECK, and *G. cookeianum* NANNFELD n. nom. (= *G. difforme* "FR." sensu CKE.). *G. glabrum* is only found in *Sphagnum*-bogs. Its paraphyses are very characteristic. Their apical cells increase often rapidly in size towards the tips. The 2–3 last cells are up to 15  $\mu$  in diameter. The tips break off in the mounts and look like a one- or two-celled teleutospore of rust fungi. *Trichoglossum hirsutum* is the only other species of the group found in *Sphagnum*-bogs. *G. glabrum* may be more common in Denmark than this scant material seems to show, but *Sphagnum*-bogs are seldom visited by mycologists.

Sjælland: Bure Mose, among *Sphagnum*, 10.10.1943, M. LANGE.

8. *Geoglossum cookeianum* NANNF.

Distribution: Europe (Great Britain, France, Italy, Germany, Denmark, Sweden).

ANDERSSON (1950) claims that *G. cookeianum* is at least a facultative sand-fungus. The Danish material supports his observation. This species may be recognised already in the field. It is more compressed than any other species known to me. Its paraphyses have some resemblance to those of *G. glabrum*, but their cells are not more than 8  $\mu$  wide.

Jylland: Thy, Tornby, in a dune, 1952, K. TOFT. Nykøbing Mors, sandy field near the sea shore, 5.10.1950, A. B. KLINGE. Sjælland: Tisvilde Hegn, in sand at a road, 31.10.1953, M. LANGE. Jægersborg Dyrehave, 7.10.1943, and another undated locality in the same wood, J. P. JENSEN. Kongelunden, 2.10.1954, M. LANGE.

### 9. *Geoglossum littorale* (ROSTR.) NANNF.

Distribution: Europe (Denmark).

This species is only found once. NANNFELDT transferred it from *Leptoglossum* to *Geoglossum* as he found some faint grayish-brown spores in the type-material. I have made the same observations. The collection looks unripe and was nearly impossible to revive in KOH. The material is probably not fully ripe and the species all together somewhat dubious.

Jylland: Vrads, Snabegård Plantage, on the shore of Snehvige Sø, 8.8.1890, (B. H. (typus) and P. H.).

### 4. *Trichoglossum* BOUD.

This genus is well characterised by its black fruit bodies, fuliginous, septated spores, and the black-brown thick-walled setae in the hymenium and on the stem. The species are macroscopically uniform and can only be distinguished by means of the spore characters. The paraphyses are of no distinctive value. NANNFELDT (1942) gives a key to all species. Only the following two species are found in Denmark:

Spores at maturity normally 15-septate, Asci 8-spored 1. *Trichoglossum hirsutum*

Spores at maturity normally 15-septate, Asci 4-spored 2. *Trichoglossum tetrasporum*

#### 1. *Trichoglossum hirsutum* (PERS. ex FR.) BOUDIER.

Distribution: Europe, North America, Asia, New Zealand.

Spores (100–)120–150–(160)  $\mu \times 6$ –7  $\mu$ .

Jylland: Kolding, E. WARMING, (B. H.). Djursland, Rugård, common, 25.10.1953, A. B. KLINGE. Glatved Kalkbakker, 27.10.1953, A. B. KLINGE. Fyn: In a bog at Skårupør, 11.9.1862, E. ROSTRUP, (B. H.). Langeland: Tranekær, in a *Sphagnum*-bog, 6.8.1953, M. LANGE. Låland: Karleby Mose, August 1862, E. ROSTRUP, (B. H.). Falster: Horreby Lyng, 1893, E. ROSTRUP and C. H. OSTENFELD. 5.11.1942, M. P. CHRISTIANSEN. Sjælland: Jægersborg Dyrehave, 7.11.1943 and 11.10.1953, M. P. CHRISTIANSEN. Ibid., J. P. JENSEN. Ibid., 11.10., 17.10. and 15.11.1953, E. BILLE-HANSEN, (8 collections). Ibid. 23.10.1953, M. LANGE. Kongelunden, between mosses at a path under *Picea*, September 1948, E. BILLE-HANSEN and M. LANGE. Kongelunden, October 1948, M. LANGE.

#### 2. *Trichoglossum tetrasporum* SINDEN & FITZPATRICK.

Distribution: U.S.A., Europe (Great Britain, Denmark).

Only one specimen in a collection of *Tr. hirsutum*. Spores: 107–138  $\mu \times$  (14)–15  $\mu$ . Septa agree with the description of SINDEN & FITZPATRICK. In some asci were seen 4 hyaline, abortive spores besides 4 normal brown ones. It may be nothing but a four-spored form of *Tr. hirsutum*.

Sjælland: Jægersborg Dyrehave, Skovriderengen, 1943, J. P. JENSEN.

*Trichoglossum variabile* (DUR.) NANNF. is found on two localities in Sweden (NANNFELDT (1942) and personal information). It is a 8-spored species, the number of septa are varying from 11–14.

*Trichoglossum walteri* (BERK. ap. CKE.) DUR. is found on two localities in Sweden. (NANNFELDT 1942). I can add a new Swedish locality: Hallands Väderø, 7.9.1952, N. F. BUCHWALD (P. H.). *Tr. walteri* has 8-spored asci. The spores are normally 7-septate, (75–)90–95(–100)  $\mu$  long.

MESSRS. N. F. BUCHWALD, M. P. CHRISTIANSEN, J. P. JENSEN and M. LANGE (all Copenhagen) and A. B. KLINGE (Randers) have placed Danish material of several species at my disposal. J. A. NANNFELDT (Uppsala) has given me Swedish material of *G. glabrum* and lend me the types of *G. elongatum* and *G. vleugelianum*. I render my best thanks for this help.

### Literature.

- ANDERSSON, O., 1950: Larger fungi on sandy grass heaths and sand dunes in Scandinavia. Bot. Not., Suppl. 2 (2): 1–89.
- DURAND, E. J., 1908: The Geoglossaceae of North America. Ann. Myc. 6: 387–477.
- 1921: New or noteworthy Geoglossaceae. Mycologia 13: 184–187.
- HOLMSKJOLD, TH., 1790: Beata ruris otia fungis danicis impensa. Vol. I, København.
- IMAI, S., 1938: Studies on the Geoglossaceae of Japan IV. The genus Microglossum. Bot. Mag. 52: 417–424.
- LIND, J., 1913: Danish fungi as represented in the herbarium of E. Rostrup. 650 pp. Copenhagen.
- LLOYD, C. G., 1916: The Geoglossaceae. Mycol. Writings 5: 1–22.
- NANNFELDT, J. A., 1942: The Geoglossaceae of Sweden. Ark. f. Bot. 30 (2): 1–67.
- ROSTRUP, E., 1892: Mykologiske meddelelser (3). Spredte iagttagelser fra årene 1889–1891. Bot Tidsk. 18: 65–78.
- SCHUMACHER, C. F., 1803: Enumeratio plantarum in partibus Sællandiae septentrionalis et orientalis. Pars posterior. København.
- SINDEN, J. W. & FITZPATRICK, H. M., 1930: A new Trichoglossum. Myc. 22: 55–61.



*Ciboria Batschiana* (ZOPF) BUCHW.  
(Syn. *Sclerotinia pseudotuberosa* (REHM) REHM)

Contribution to the Discussion of the Nomenclature  
of the Species

By N. FABRITIUS BUCHWALD

In two previous papers (BUCHWALD, 1947 and 1949) I have already called attention to the fact that the first validly published name for the cup-fungus usually called *Sclerotinia pseudotuberosa* (REHM) REHM, is the far less familiar *Sclerotinia Batschiana* ZOPF, which therefore in conformity with the International Code of Botanical Nomenclature must be regarded as the legitimate name of the fungus.<sup>1)</sup>

In my paper of 1949 I promised to state the grounds for this change of name later on, adding a detailed discussion of the nomenclature of the species. In what follows I fulfil this promise.

I. Nomenclature.

1947. *Ciboria Batschiana* (ZOPF) BUCHW., Friesia 3, p. 255, 1947. – BUCHWALD, Contrib. Dept. Pl. Path., No. 32, Roy. Vet. Agric. Coll., Copenhagen, pp. 99, 159, 164 (1949).

A. Synonyma.

1. Status ascophorus.

a. *Quercus*.

1873<sup>2)</sup>. *Ciboria pseudotuberosa* REHM, Ascomyceten, no. 106 a (et b) (*nomen nudum*). – REHM, 26. Ber. naturh. Ver. Augsburg, p. 29 (1881); WINTER, Hedwigia 21, pp. 8, 36 (1882); PATOUILLARD, Tab. analyt. fung., tab. 171, fig. 378 (1885); SACCARDO, Syll. fung. 8, p. 201 (1889); OUDEMANN, Ned. Kruidk. Arch., 3 ser. II, p. 208 (1901); Enum. syst. fung. 2, p. 823 (1920).

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<sup>1)</sup> It is to be regretted that F. J. SEAVER in his monograph of the North American Cup-fungi (Inoperculates) (1951) has not taken account of this change in nomenclature but still calls the fungus *Sclerotinia pseudotuberosa* REHM.

<sup>2)</sup> non 1870!

1876. *Peziza pseudotuberosa* (REHM) COOKE, Grevillea 4, p. 132, pl. 65, fig. 288 (*nomen nudum*). – ELLIS, N. Amer. Fungi no. 983 (1883).
1879. *Sclerotinia Batschiana* ZOPF in ZOPF & SYDOW, Mycoth. March. no. 50. – ZOPF, Die Pilze, pp. 19, 206, 233, 236 and 281 (1890).
1880. *Peziza (Hymenoscypha) pseudotuberosa* (REHM) in PHILLIPS & PLOWRIGHT, Grevillea 8, p. 102.
1881. *Peziza (Aleuria) glandicola* DOASS. & PAT., Champ. fig. et desséchés, no. 13. – ROUMEGUÈRE, Rev. Myc. 3, no. 10, p. 49 (1881) and no. 11, p. 21 (1881); DOASSANS & PATOUILARD, Bull. Soc. Bot. France 27, p. 356 (1881, non 1880).
1885. *Ciboria (Stromatinia) pseudotuberosa* (REHM) BOUD., Bull. Soc. Myc. France 1, p. 115.
1887. *Hymenoscypha pseudotuberosa* (REHM) PHILL., Man. Brit. Disc., p. 119; 2 ed., p. 119 (1893).
1887. *Phialea glandicola* (DOASS. et PAT.) QUÉLET, Assoc. Franç. l'Avance. Sci. Congrès de Toulouse 16, p. 587.
1893. *Sclerotinia pseudotuberosa* (REHM) REHM, Discomyceten, p. 809. – TUBEUF, Pflanzenkrankheiten, p. 284 (1895); DURAND, Bull. Torr. Bot. Club 27, p. 481 (1900); ROSTRUP, Plantepatologi, p. 552 (1902); LIND, Danish Fungi, p. 111 (1913); REHM, Ber. Bayer. Bot. Ges. 15, p. 234 (1915); FERDINANDSEN & WINGE, Mykol. Ekskursionsflora, p. 282 (1928); 2. Udg., p. 390 (1943); FERDINANDSEN, Smitsomme Sygdomme hos Skovtræerne (Ref. ved N. F. BUCHWALD), p. 34 (1928); NANNFELDT, Die inoperculaten Discomyceten, p. 308 (1932); BUCHWALD, Friesia 1, p. 57 (1932); KILLERMANN, Kryptogam. Forsch. 2, p. 279 (1935); LUNDELL & NANNFELDT, Fungi exs. suecici, p. 36 (1938); FERDINANDSEN & JØRGENSEN, Skovtræernes Sygdomme, p. 211 (1938-39).
1907. *Stromatinia pseudotuberosa* (REHM) BOUD., Discomyc. d'Eur., p. 108.

b. *Castanea*.

1920. *Sclerotinia castaneae* PEYRONEL, Rendiconti R. Accad. Lincei, Roma, 29, Ser. 5 (2° Sem.), p. 326 (*nomen nudum*).
1920. *Sclerotinia pseudotuberosa* (REHM) REHM in PEYRONEL, ibidem p. 324. – VOGLINO, La Difesa delle Piante 8, p. 1 (1931); ARNAUD & BARTHELET, Ann. Épiphyt. et Phytogénét. 1, p. 121 (1936).

2. Status microconidiophorus.

a. *Quercus*.

1913. *Sphacelia* sp. LIND, Danish Fungi, p. 108 (non ZOPF, 1880).

b. *Castanea*.

1905. *Rhacodium cellare* PERS. sensu PEGLION, Rendiconti R. Accad. Lincei, Roma, 14, Ser. 5 (2° Sem.), p. 740.
1908. *Harziella castaneae* BAINIER, Bull. Soc. Myc. France 24, p. 90. – PEYRONEL, Rendiconti R. Accad. Lincei, Roma, 25, Ser. 5 (2° Sem.), p. 459 (1916).
1919. *Rhacodiella castaneae* (BAIN.) PEYRONEL, Staz. Sperim. Agrar. Ital. 52, p. 36 and 39. – PEYRONEL, Rendiconti R. Accad. Lincei, Roma, 29, Ser. 5 (2° Sem.),

p. 324 (1920); CLEMENTS & SHEAR, Genera of Fungi, p. 210 and 394 (1931); VOGLINO, La Difesa delle Piante 8, p. 1 (1931); La Difesa delle Piante 9, p. 1 (1932); SERVAZZI, *ibid.* 12, p. 191 (1935); ARNAUD & BARTHELET, C. R. Acad. Agric. France 22, p. 48 (1936); Ann. Épiph. et Phytogénét. 1, p. 121 (1936); Bull. Soc. Myc. France 52, p. 63 (1936); BUCHWALD, Fungi imperfecti p. 81 (1939).

## B. Icones.

### a. *Quercus*.

COOKE, Grevillea 4, pl. 65, fig. 288, 1876. (*Peziza pseudotuberosa*).

ZOPF in ZOPF & SYDOW, Mycoth. March., no. 50, figs. 1–8, 1880. (*Sclerotinia Batschiana*).

DOASSANS & PATOUIILLARD, Champ. fig. et desséchés, no. 13, 1881. (*Peziza glandicola*).

PATOUIILLARD, Tab. anal. fig., tab. 171, fig. 378, 1885. (*Ciboria pseudotuberosa*).

PHILLIPS, Man. Brit. Discom., tab. 5, fig. 25. (*Hymenoscypha pseudotuberosa*).

QUÉLET, Assoc. Franç. l'Avance Sci. 16, tab. 21, fig. 16, 1887. (*Phialea glandicola*).

REHM, Discomyceten, p. 800, figs. 1–5, 1893. (*Sclerotinia pseudotuberosa*).

DURAND, Bull. Torr. Bot. Club 27, tab. 31, fig. 11, 1900. (*Sclerotinia pseudotuberosa*).

ROSTRUP, Plantepatologi, fig. 234, 1902. (*Sclerotinia pseudotuberosa*).

BOUDIER, Icon. mycol. 3, tab. 480, 1906–07. (*Stromatinia pseudotuberosa*).

FERDINANDSEN & WINGE, Mykol. Ekskursionsflora, fig. pag. 282, 1928. (*Sclerotinia pseudotuberosa*).

FERDINANDSEN & JØRGENSEN, Skovtræernes Sygdomme, fig. 89, 1938–39. (*Sclerotinia pseudotuberosa*).

### b. *Castanea*.

BAINIER, Bull. Soc. Myc. France 24, tab. 9, figs. 1–5, 1908. (*Harziella castaneae*).

PEYRONEL, Staz. Sperim. Agrar. Ital. 52, tab. 1–4, figs. 1–14, 1919. (*Rhacodiella castaneae*).

ARNAUD & BARTHELET, Ann. Épiphyt. et Phytogénét. 1, fig. 1 (pag. 123), fig. 2 (p. 128) and fig. 3 (p. 129), 1936. (*Sclerotinia pseudotuberosa* and *Rhacodiella castaneae*).

ARNAUD & BARTHELET, Bull. Soc. Myc. France 52, fig. 1, C, D (pag. 64), fig. 3, C (p. 67) and fig. 4, C (p. 68), 1936. (*Rhacodiella castaneae*).

## C. Exsiccata.

REHM, Ascom. no. 106a & b, 1872. (*Ciboria pseudotuberosa*).

ZOPF & SYDOW, Mycoth. March. no. 50, 1880. (*Sclerotinia Batschiana*).

\*) RABENHORST & WINTER, Fungi europ. et extraeurop. no. 2649, 1881. (*Ciboria pseudotuberosa*) (teste REHM, 1893).

\*) ELLIS, N. Am. fungi no. 983, 1883. (*Peziza pseudotuberosa*) (confirm. H. H. WHETZEL *in litt.* 9.2.1940).

SYDOW, Mycoth. germ. no. 996, 1911. (*Sclerotinia pseudotuberosa*).

LUNDELL & NANNFELDT, Fungi exs. suecici no. 595, 1938. (*Sclerotinia pseudotuberosa*).

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\*) Material not seen by the author.

## II. Contribution to the Discussion of the Nomenclature of the Species.

From the list of synonyms above it will appear that only three names can come into consideration in estimating which species-name is the legitimate one, namely: *Ciboria pseudotuberosa* REHM, *Sclerotinia Batschiana* ZOPF, and *Peziza glandicola* DOASS. & PAT. The rest of the names entered in the list of synonyms—apart from the far later name of the conidial stage of the fungus—are merely *combinationes novae*, and are therefore of no interest in this context.

A comparison of the diagnoses<sup>1)</sup> of the above-mentioned species will at once show that we are concerned with one and the same species of fungus, a fact about which there has, indeed, never been any doubt. This will appear amongst other things from the circumstance that REHM already in his description of *Ciboria pseudotuberosa* (1881) gave both *Peziza glandicola* and *Sclerotinia Batschiana* as synonyms (cp. p. 24). It may be added that the author has been able to examine type material<sup>2)</sup> both of *Ciboria pseudotuberosa* and of *Sclerotinia Batschiana* and to verify the identity of these two species, whereas it has not been possible to procure type material of *Peziza glandicola*.

Since the three species-diagnoses were published at about the same time, namely in the period around 1880, and even in the case of two of them in exsiccate works, only a close examination of the literature has rendered it possible to establish with certainty the time of the publication of the three diagnoses in question.<sup>3)</sup>

### 1. *Ciboria pseudotuberosa* REHM

The first place where the cup-fungus of the oak is introduced into the mycological literature is on a label in the exsiccate work "Ascomyceten"

<sup>1)</sup> The specific diagnoses are reproduced on pp. 24, 27, and 29.

<sup>2)</sup> The type material has kindly been lent me by the late Professor Dr. E. ULBRICH, the Botanical Museum of Berlin.

<sup>3)</sup> Exsiccatates are often very deficient in information about the time of their publication; if to this is added the unfortunate fact that the exsiccate is divided and the individual numbers are distributed over their respective systematic places, as so often happens in the herbaria of botanical museums, one is in fact confined to a study of the periodical literature if one wants to discover the year (and perhaps the date) of publication of a particular diagnosis. This circumstance induces the author to make the following practical proposal to the publishers of exsiccata, namely



Fig. 1. Type specimen of *Ciboria pseudotuberosa* REHM (collected autumn 1870) from E. REHM's exsiccate "Ascomyceten", No. 106 (1873) and another collection of *Ciboria pseudotuberosa* from autumn 1881 (from the same exsiccate, No. 106b). It appears plainly that the name *Ciboria pseudotuberosa* is not accompanied by any diagnosis, that is to say, it occurs here as a *nomen nudum*.—Materials in the Botanical Museum of Berlin and photographed by the late Professor, Dr. E. ULBRICH.

that they should add the date of publication on the labels of the exsiccate when new species are published. It should be kept in mind that exsiccata, according to their nature, are to be regarded as books, being, like these, always issued in a definite number (small, it is true) consisting of uniform specimens, and so it is only natural to demand that the exsiccata should be treated like books and so be furnished with the year of their publication (and if possible the date). This simple procedure will not only save systematists a very time-consuming task, but also, which is still more important, entirely remove the uncertainty now often prevailing as regards the year when fungus-exsiccata were published.

prepared by REHM. The fungus (sclerotia with apothecia) is published as No. 106 in fasc. III, and the label bears the following inscription:

“*Ciboria pseudotuberosa* mihi nov. spec. Auf faulenden Cotyledonen von Eicheln am Waldrande bei Sugenheim in Franken. Herbst 1870. Dr. REHM.”<sup>1)</sup>)

From this it appears plainly that the name *Ciboria pseudotuberosa* is not accompanied by any diagnosis, that is to say, it occurs here as a *nomen nudum*. A diagnosis is not met with until several years later, namely in 26. Bericht Naturh. Ver. Augsburg (1881), in which REHM issued the descriptions of the *Ascomycetes* published in the first 11 fascicles of his exsiccate. On pp. 28–29 is seen the following Latin diagnosis of *Ciboria pseudotuberosa*:

“106. *Ciboria pseudotuberosa* REHM nov. spec. 1870! Syn. *Sclerotinia Batschiana* ZOPF 1880! in ZOPF et SYD. myc. march. 50 c. icon. *Peziza glandicola* DOASS. in Revue myc. Nr. 10 p. 49. – cfr. *Grevillea* IV, pl. 65. f. 288.

*Perithecia gregaria*, 2 cm. long., stipitata, stipite tenui, subflexuoso, sicco plerumque longitudinaliter striato, olivaceo, sicca infundibuliformia, subcomplicata, olivaceofusca, humida explanata, subpatellaeformia, disco livido-fusco, 5–7 mm. diam. Asci clavati, 8 spori, – 120/6. Sporidia obtuse-oblonga vel ovata, glabra, 1 cellularia, hyalina, 8–9/4–4.5, monosticha in superiore asci parte. Paraphyses filiformes, superne sensim—3 mikr. incrassatae, hyalinae. Jod coeruleescit apicem ascorum.

*Ad cotyledones putridas quercuum in sylvis prope Windsheim (Franconia bav.)*”.

From the above diagnosis it will be seen that REHM himself regards the name *Ciboria pseudotuberosa*, given by him to the tuberous cup-fungus of the oak, as the right one, evidently because it is the earliest. The notes of exclamation added both after the year 1870 and after the 10 years later name *Sclerotinia Batschiana* ZOPF from 1880 will be noticed.

First, as regards the year 1870 the impartial reader will at once be likely to take the view that this year was the year of publication for *Ciboria pseudotuberosa*. That is not the case, however. For fasc. III of “*Ascomyceten*” was not published until the spring of 1873, possibly already in the autumn of 1872. This appears amongst other things from the fact that REHM himself in “*Flora*”, 56. Jahrg., No. 13, p. 206 (issued May 1, 1873), informs the mycological reading public that now fasc. III

<sup>1)</sup> It may be added that under the serial number 106b in the same exsiccate there is distributed another but much later find whose label bears the inscription: “106b. *Ciboria pseudotuberosa* REHM. An faulenden Cotyledonen von Eicheln. Thiergarten bei Berlin. Herbst 1881. SYDOW.”



of his *Exsiccata* has appeared, and that of new species this fascicle contains amongst others *Ciboria pseudotuberosa*. That 1873 was the year when fasc. III was published is further supported by the fact that in "Botanischer Jahresbericht", Jahrg. 1 (issued in 1874) which contains mycological literature for the year 1873, there is on p. 47 a list of the species of fungi in fascels. III and IV (Nos. 101–200) of REHM's "Ascomyceten". In LINDAU & SYDOW: *Thesaurus litteraturae* it is indeed stated that fasc. III (Nos. 101–150) was published already in 1872. But whether the year of publication was 1873, or possibly 1872, the fact remains that at any rate it was not 1870. Therefore, when REHM in his diagnosis of *Ciboria pseudotuberosa* mentions 1870, he was evidently thinking of the year when it was collected, which was that very year, 1870 (cf. above the inscription on the label). The specification of the year 1870 was all the more unfortunate since it was copied in the publications of other authors on *Ciboria pseudotuberosa*, thus by WINTER (*Hedwigia* 21, p. 36, 1882) and SACCARDO (*Syll. fung.* 8, p. 201, 1889), REHM's diagnosis being reprinted without comment in both places.

Summing up we may then establish the following chronology for *Ciboria pseudotuberosa*:

In 1870 (autumn) REHM collected material of *Ciboria pseudotuberosa*.

In 1873 (possibly already in 1872) fasc. III of "Ascomycetes" was issued with *Ciboria pseudotuberosa* placed under No. 106, but the name was only published as a "*nomen nudum*".

Not until 1881 did REHM issue a valid diagnosis and the latter year is therefore the actual publication-year for *Ciboria pseudotuberosa*.

In this connection it should, however, be mentioned that even though the diagnosis of *Ciboria pseudotuberosa* only dates from 1881, the English mycologist M. C. COOKE, as early as 1875/76, published a plate ("Grevillea" IV, plate 65) with figures of asci, paraphyses, and ascospores of a number of *Peziza* species, among which *Peziza* (i. e. *Ciboria*) *pseudotuberosa* REHM was also included (Fig. 288). An informative text, not to speak of a description of the species with statement of spore dimensions etc., is entirely lacking. The figures themselves must, however, be considered too incomplete to supply the place of a diagnosis, since both asci and spores are very little characteristic in *Ciboria pseudotuberosa* and are too much like the asci and spores of other *Peziza* species to give any systematic lead. Finally it must be called to mind that the figures are not derived from REHM but from COOKE who, if the figures were really to be considered equivalent to a diagnosis, must then be regarded as the author of the species. The present writer, however, is of opinion that COOKE's figures

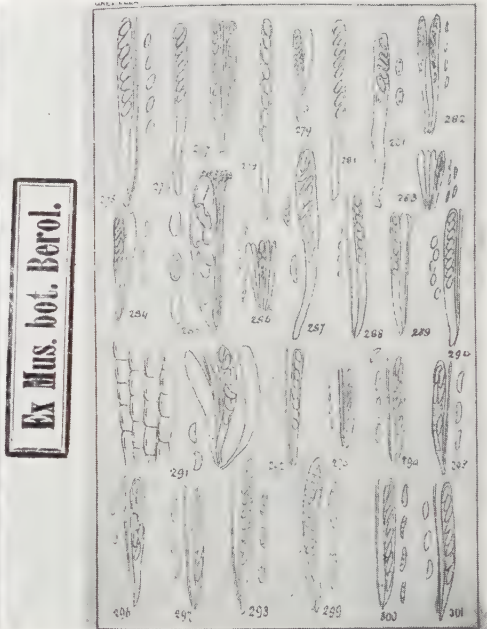
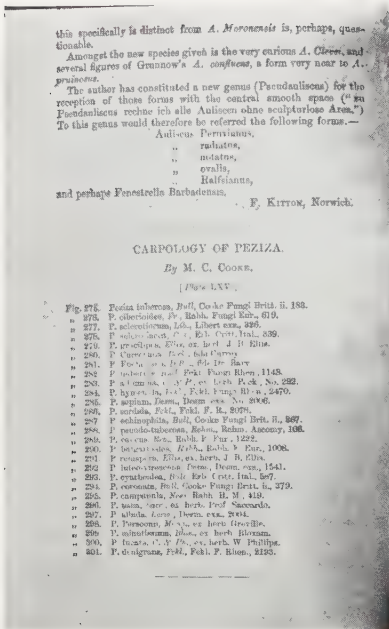


Fig. 2. Page 132 and plate 65 in "Grevillea" IV, 1875/76 with figures of asci, paraphyses, and ascospores of a number of *Peziza* species, among which *Peziza (Ciboria) pseudotuberosa* REHM (Fig. 288). *Peziza pseudotuberosa* is not accompanied by any diagnosis, that is to say, it occurs here as a *nomen nudum*.—Photographed by the late Professor, Dr. E. ULBRICH, Berlin.

of *Peziza pseudotuberosa* do not meet the requirements of the Code of Nomenclature, Art. 52 (1950) in which it says:

"The name of a species or of a subdivision of a species of recent plants is not validly published unless it is accompanied . . . by (2) a plate or figure with analyses showing *essential*<sup>1)</sup> characters".

*Peziza pseudotuberosa* (REHM) COOKE must therefore be referred to *nomina nuda*.

We will now proceed to examine the years of publication of the other two species which REHM (1881) mentions as synonyms in his diagnosis, namely *Peziza glandicola* and *Sclerotinia Batschiana*. Already from the fact that they are mentioned by REHM it will appear that they are older than the diagnosis of *Ciboria pseudotuberosa*. Two questions at once arise. (1) Have the names in question been published in connection with

<sup>1)</sup> Present writer's italics.

a valid diagnosis? (2) If so, which of the two names was published first and is thus the legitimate name? We will first consider *Peziza glandicola*.

## 2. *Peziza glandicola* DOASS. & PAT.

In Bull. Soc. Bot. de France 27: 355–356, under the title of “Espèces nouvelles de champignons (*Polyporus favoloides*, *Peziza glandicola*)” DOASSANS & PATOUILLARD published (p. 356) a specific description of *Peziza glandicola*:

“*Peziza glandicola*.—Gregaria; patella ( $\frac{1}{4}$  unc.) haud crassa, ochraceo-brunnea, extus pruinosa; stipite ( $\frac{1}{2}$  unc.) fusco, pruinoso, gracili, elongato; ascis tenuibus, longis; sporis oblongis, hyalinis, sine nucleo. — Habitat in silvis, autumno, in glandium superiore anno-cotyledonibus jampridem nigrefactis.”<sup>1)</sup>

Since the above-mentioned volume 27 of Bull. Soc. Bot. France has the year 1880 on the title-page one would be inclined to regard that year as the year of publication for *Peziza glandicola*. Several facts, however, militate against this presumption. In the first place it is stated that the above-mentioned paper “Espèces nouvelles de champignons” has been submitted at a meeting of the Société Botanique de France which was held as late in the year as the 10th December 1880. In the second place the authors mention that *Peziza glandicola* has been published under the serial number 13 in the Exsiccata work “Les Champignons figurés et desséchés”. Unfortunately this comparatively little known exsiccata is neither to be found in the Botanical Museum of Copenhagen nor in the Botanical Museum of Berlin,<sup>2)</sup> so that the author was not able to examine it himself<sup>3)</sup>, but had to resort exclusively to what the literature could inform him concerning its publication.

From a literature list in No. 37 of “Botanische Zeitung”, Jahrg. 38, p. 640 (issued September 10, 1880) it is seen that species No. 1 (accompanied by a plate with text) has just been published. From this therefore it is clear that the exsiccata work had begun to appear about the 1st September 1880; in the same place in No. 49, p. 831 (issued Dec. 3, 1880)

<sup>1)</sup> According to my exsiccata notes vol. 1 of “Champ. fig. et desséchés” dates from 1882. Can this be right? If that year is right a possible diagnosis here cannot compete as to age with the diagnosis in Bull. Soc. France 27, which dates from 1880.

<sup>2)</sup> According to the kind communication of the late Professor Dr. E. ULBRICH, Berlin.

<sup>3)</sup> Nor does REHM seem to have seen this exsiccata as he does not refer to it either in his diagnosis of *Ciboria pseudotuberosa* (1881) or later in his treatment of the *Discomycetes* (“RABENHORST” 1893).

it is stated that 9 numbers in all have now been published. Finally it appears from a review (by C. ROUMÉGUÈRE) in "Revue Mycologique" III, No. 10, pp. 48–49 (issued April 1, 1881), in which there is a brief statement of the object and contents of the exsiccata,<sup>1)</sup> that now the number of species published has reached 22. As No. 13 is given: *Peziza (Aleuria) glandicola* sp. nov., and in a footnote is printed a Latin diagnosis of the fungus, which no doubt has been copied from the label of the exsiccate. Apart from a few linguistic divergencies (probably misprints in Rev. Myc.!) it is identical with the above-quoted diagnosis from Bull. Soc. Bot. France 27, p. 356.

From the particulars communicated here concerning the publication of the exsiccate it can, in other words, be computed that the diagnosis of the species was published in January, possibly in February 1881. The above-mentioned paper "Espèces nouvelles de champignons", in which No. 13 in the exsiccata is referred to, must then have been published after that time! When, then, did the paper in question appear? The reply to this query is given in a review by ROUMÉGUÈRE, "Nouvelles espèces de champignons observées par MM. DOASSANS & PATOUILLARD", printed in Rev. Myc. III, No. 11, pp. 21–22, 1881 (issued July 1, 1881). For on p. 21 we find the following statement:

"Le dernier bulletin paru des séances de la Soc. Bot. de France contient (T. 27, p. 355) la diagnose du *Peziza glandicola*, qui nous avons déjà donné (Revue p. 48)."

So from this we may draw the conclusion that the paper in Bull. Soc. Bot. Fr. must have been issued in the period between April 1, 1881 (when No. 10 of Rev. Myc. was published) and July 1, 1881.

Summing up we may then establish the following chronology for *Peziza glandicola*:

In 1880, October, DOASSANS & PATOUILLARD collected material of *Peziza glandicola* in the Chaville forest in the environs of Paris.

In 1880, December 10, DOASSANS & PATOUILLARD submitted this find of the fungus (together with others) at a meeting of the Société Botanique de France.

In 1881, January-February, material of the fungus was issued as No. 13 in their exsiccata under the name of *Peziza glandicola*, accompanied by a Latin diagnosis.

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<sup>1)</sup> It is stated amongst other things that the work will be issued in series of 50 numbers, each number comprising one species of fungus, accompanied by a plate with text and figures. It is intended to issue about 4 numbers a month.



In 1881, April 1, the first accurately dated diagnosis of the species was published (in Rev. Myc. No. 10, by C. ROUMÈGUÈRE).

In 1881, in the interval April 1–July 1, DOASSANS & PATOUILLARD's paper "Espèces nouvelles de champignons" was published in Bull. Soc. Bot. de France.

It will be seen then that the diagnosis of *Peziza glandicola* was published no less than three times in the course of the first half of the year 1881, the first time probably already in January–February. Since REHM, as mentioned above (pp. 22, 24), gives *Peziza glandicola* among the synonyms of *Ciboria pseudotuberosa*, the diagnosis of which was also published in 1881, it is at any rate given that *Peziza glandicola* is older and consequently has the priority over *Ciboria pseudotuberosa*.

We now turn to the third name that has been given to the tuberous cup-fungus of the oak, *Sclerotinia Batschiana*.

### 3. *Sclerotinia Batschiana* ZOPF

The diagnosis of this species was published under the serial number 50 in ZOPF & SYDOW "Mycotheca Marchica". The label is lithographed, not written by hand in ink. The diagnosis<sup>1)</sup> runs as follows:

"50. *Sclerotinia Batschiana* nov. spec.

*Mycelium fructus (cotyledones) Quercus pedunculatae in sclerotia transformat atra, dura, e quibus anno proximo nascuntur fructus ascophori, pezizaeformes, sessiles vel plus minus longe pedicellati, basi atrii, superne brunnei. Cupula initio cupuliformis, dein explanata vel margine reflexa, cinnamomea, glabra; discus concolor, saepe sporis ejaculatis albido-pruinosis. Asci anguste lineares-clavati, longe pedicellati, 8 spori. Sporae simplices, ellipsoideae, ovatae v. oblongae, magnit. diversae, hyalinae. Paraphyses graciles, basi parce ramosae, filiformes, septatae, hyalinae, ascos subaequantes. Conidia (!) in sterigmatibus minutissimis (iis *Pez. tuberosa* et *Sclerotior. similibus*) nascentia, sphaerica vel ovata, perexigua, guttula oleosa instructa, hyalina.*

*Seit Aug. 1875 von mir alljährlich im Thiergarten b/Berlin beobachtet, daselbst eine sehr bedeutende Anzahl von Eicheln vernichtend und daher von besonderem, forstlichem Interesse. An genanntem Orte Herbst 78. leg P. SYDOW. Dr. W. ZOPF."*

According to REHM (26. Ber. Naturh. Ver. Augsburg, cf. above p. 24) the year of publication was 1880, but both LINDAU & SYDOW: "Thesaurus

<sup>1)</sup> The diagnosis is accompanied by a plate with 8 figures in all, of which figs. 1 and 2 show sclerotia with apothecia, fig. 3 ascus with 8 spores, fig. 4 paraphysa, fig. 5 ascospores ( $\frac{540}{1}$ ), fig. 6 germinating ascospore, fig. 7 ascospores germinating with phialide with microconidia, fig. 8 hypha with phialides. Some of the figures are reproduced by REHM in "Discomyceten", p. 800 (1893).



Ex Mus. bot. Berol.

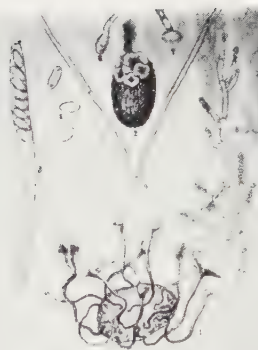


Fig. 1. Sclerotinia Batschiana Marchica

50 Sclerotinia Batschiana n. sp.

*Mycelium* fructus (cotyledones) laticornis pedunculatae in  
sclerotio transformatae, durae, ex quibus anno proximo  
nascentibus fructus ascosporii, peritheciae, ascus vel  
his minus longe, necesse est, huius alii superne laticornis  
quarta parte vixit, formis etiam exsternatis vel marginis re-  
pleti, annuati, albae, discus concolor, saepe sporis  
punctatis albis-pruinosis. Bei anguste lineares, cha-  
racte longe pedunculatae, sporis saepe singulis, thaxi-  
dus, vixit o. oblongae, magnit. diversae, hyalinae. Perithe-  
ciae graciles, basi parce ramosae, filiformes, septatae, hyalinae,  
nec subsaccatae. Conidia in sterigmatibus multatis  
fio. In tuberosae et Sclerotia similibus nascentibus, sphaerice  
collocata, perithecia gellata, flosa instructa, hyalina.

Im Jahr 1875 war mir altpflanzlich im Tiergarten (Berlin)  
beobachtet, dasselbe eine sehr bedeutende Anzahl von Eichen vor-  
sachend, und war von besondern, dorthin im Winter.

Angewandt am 1. April 1875, 1875, 1875.

Typus

No. 11. 1875

Typus - Erklärung

1. Sclerotium mit langgestreckten, 2. von oben gesehen mit  
abwärtigen Seiten 3. Peritheciae 4. Peritheciae 5. Peritheciae 6. Peritheciae  
7. Anhang mit Conidia 8. Conidia 9. Conidia 10. Conidia

Fig. 3. Type specimen of *Sclerotinia Batschiana* ZOPF from ZOPF & SYDOW, Mycotheca Marchica, No. 50 (1879). The diagnosis of the label is lithographed, not written by hand in ink. – Material in the Botanical Museum of Berlin and photographed by the late Professor, Dr. E. ULBRICH.

literaturae" and BARNHART's "Bibliography" to Vol. 9, Part 6 of "North American Flora" (1916) give the year 1879. An investigation of the literature shows that the latter year must be the right one. For from "Verh. botan. Ver. Prov. Brandenburg" for 1879 (issued 1880) it appears that W. ZOPF, at the 71st "Sitzung", (whose proceedings are printed on pp. 164–184) on the 19th December 1879, submitted the 1st Century of the exsiccata "Mycotheca Marchica" started by him in collaboration with P. SYDOW; from which it quite naturally follows that this century must already have been lying completed at the close of 1879. At the presentation ZOPF, incidentally, made the following comments concerning the figures on the accompanying plates (10 in all), namely that these had been produced on the basis of studies on the developmental history, which, as far as *Sclerotinia Batschiana* is concerned, amongst other things shows the genetic connection between the conidia and the ascospores.

We have now concluded our review of the three species and from this it will appear that the following publication-years may be established for the diagnoses:

- 1879 (ultimo): *Sclerotinia Batschiana* ZOPF
- 1881 (primo): *Peziza glandicola* DOASS. & PAT.
- 1881: *Ciboria pseudotuberosa* REHM

There can now be no doubt that *Sclerotinia Batschiana* ZOPF has the priority and therefore, according to the Code of Nomenclature in force, is the legitimate name. Since the present author is of opinion that the species is no *Sclerotinia* but a *Ciboria*, he has already in 1947 (p. 255) referred it to this genus under the combination *Ciboria Batschiana* (ZOPF) BUCHW. In this connection he may further refer to the fact that already in 1949 (pp. 162–165) he suggested that *Ciboria* should be divided into two subgenera, namely *Euciboria* BOUD. whose type-species should be *Ciboria caucis* (REBENT.) FCKL., and *Stromatinia* BOUD. with the type-species *Sclerotinia Batschiana* (ZOPF) BUCHW., or perhaps *Pseudociboria* subg. n., if it should turn out that H. H. WHETZEL (1945) was right in his conjecture that *Stromatinia* BOUD. must be regarded as a separate genus with *Peziza rapulum* BULL. as type-species. According to GROVES & DRAYTON's recent investigations on *Stromatinia narcissi* DRAYTON & GROVES (1952), *Stromatinia* BOUD. must be regarded as a good independent genus. So the above-mentioned subgenus with *Ciboria Batschiana* (ZOPF) BUCHW. as the type-species should be named *Pseudociboria* subg. n.

## Summary.

The cup-fungus that attacks and mummifies acorns is usually called *Sclerotinia pseudotuberosa* (REHM) REHM in the literature. Already in 1947 and 1949 the present writer pointed out that *Ciboria pseudotuberosa* REHM (1873) as well as *Peziza pseudotuberosa* (REHM) COOKE (1876) are *nomina nuda* and therefore invalid. The first name which is accompanied by a diagnosis (even with figures), is *Sclerotinia Batschiana* ZOPF (1879), which must therefore be regarded as the correct name of the fungus. Since the species, however, in the author's opinion is no *Sclerotinia* but a *Ciboria*, it was already in 1947 referred to that genus under the combination *Ciboria Batschiana* (ZOPF) BUCHW.

## Literature.

- BUCHWALD, N. FABRITIUS, 1947: Sclerotiniaceae. I. *Ciboria*, *Rutstroemia*, *Myriosclerotinia* g. n. og *Sclerotinia*. *Friesia* 3: 235–330.
- 1949: Studies in the Sclerotiniaceae. I. Taxonomy of the Sclerotiniaceae. *Contrib. Departm. Plant Pathology* No. 32, 138 pp. The Royal Vet. Agricult. Coll., Copenhagen.
- COOKE, M. C., 1875–76: *Carpology of Peziza*. *Grevillea* 4: 132, plate 65.
- DOASSANS, E. & PATOUILLARD, N., 1880–81: *Les champignons figurés et desséchés*. No. 1–44. Paris.
- 1881: *Espèces nouvelles de champignons (Polyporus favoloides, Peziza glandicola)*. *Bull. Soc. Bot. France* 27: 355–356.
- DRAYTON, F. L. & GROVES, F. W., 1952: *Stromatinia narcissi*, a new, sexually dimorphic discomycete. *Mycologia* 44: 119–140.
- REHM, H., 1873: *Ascomyceten*. Fasc. III (Nr. 101–150).
- 1881: *Ascomyceten*. In *getrockneten Exemplaren herausgegeben*. Fasc. I–XI. 26. Ber. d. naturhist. Ver. in Augsburg: 1–132.
- SEAYER, FRED JAY, 1951: *The North American Cup-fungi (Inoperculates)*. 428 pp. New York.
- WHETZEL, H. H., 1945: A synopsis of the genera and species of the Sclerotiniaceae, a family of stromatic Inoperculate Discomycetes. *Mycologia* 37: 648–714.
- ZOPF, W. & SYDOW, P., 1879: *Mycotheca Marchica*. *Centurie I*. Berlin.

# Natural Populations of *Pulsatilla* in Zealand

By TYGE W. BÖCHER

## 1. Introduction.

Two species of *Pulsatilla* occur in Zealand, viz. *P. pratensis* and *vulgaris*. *P. pratensis* is abundant on sandy soil in grasslands along the sea but it has also many inland stations on hills covered with dry grassland. *P. vulgaris*, on the other hand, is a very rare species; it has now only one station, the hills at Villingeröd, where it grows abundantly. Descriptions of the different plant communities which contain the two species may be found in BÖCHER (1945). In both species the variability is striking, but in *P. pratensis* the manner of variation and its range changes from one station to another.

The two species belong to two different species complexes which, however, are closely related and may have a common origin (see ZÄMELS & PAEGLE (1927)).

The *P. pratensis*-complex includes *P. pratensis* with its ssp. *nigricans* (or var. *patula*), *P. montana* with its ssp. *rubra*, *P. balcana*, and probably *P. donetzica*, which according to KOTOV (1940) comes very close to *P. montana*.

The *P. vulgaris*-complex comprises *P. vulgaris* with a multitude of subspecies (*germanica*, *gotlandica*, *polonica*, *hispanica*, and *grandis*), further *P. turczaninowii* and probably *P. bulgarica* (VELENOVSKY) mentioned by ROSENTHAL (1936, pp. 810–811).

## 2. Colour of the Perianth.

*P. vulgaris*: Among 171 individuals, which were studied and compared with a horticultural colour chart (WANSCHER, 1953), 85 per cent had violet flowers, 8.3 per cent bluish violet and 6.3 per cent almost blue flowers; only 0.6 per cent had purplish violet flowers; the great majority of the violet or bluish violet flowers were dark, but a few were pale (1.8 per cent)

or very pale violet (2.3 per cent). No white-flowered individuals were observed, but such individuals were described by ZIMMERMANN (1934, p. 214) who found them as segregants in  $F_2$  after crossings between different *P. vulgaris* races. The peculiar blue flowers which resembled *Gentiana* flowers did not always have quite blue leaves, the lower parts having violet spots or being almost violet while the tips were quite blue. Blue flowers occurred only in a limited area where the density of the species was extremely high.

*P. pratensis*: The colour variation of the perianth has long been discussed. As early as 1911 OSTENFELD criticized the opinions of BECK (1890) and v. HAYEK (1904) who believed two species to be covered by the name *P. pratensis*, viz. a plant with pale-violet flowers (*P. pratensis* s. str.) and another with dark or blackish violet flowers (*P. nigricans*). In Denmark both races occur together in several localities and nothing has been found to corroborate the view that two separate species exist. OSTENFELD's view was shared by KRAWIEC (1932), JUZEPČUK (1937), and JALAS (1950). The latter treats the dark violet race as a variety of *P. pratensis* (var. *patula*), thus following PRITZEL (1841).

Examinations of the perianth colour in a number of populations from Zealand (and for comparison one from N. Jutland) are listed in Tables 1-2, arranged according to percentage of individuals with dark or blackish violet flowers. It will be seen that the dark *nigricans*-type is particularly frequent on basic or neutral diluvial sands, while the pale *eupratensis*-type is most frequent on acid alluvial sands or drift sand. The dominance of *nigricans* seems to be correlated with the occurrence of eastern species like *Cynanchum vincetoxicum*, *Potentilla heptaphylla*, *Hypochoeris maculata*, and *Filipendula hexapetala*. On the other hand, *eupratensis* may be followed by increased frequency of *Corynephorus canescens*, *Carex arenaria*, *Jasione montana* and other species indicating poor soil. In addition to the populations listed in the tables it may be mentioned that dominance of dark flowers was observed also at Høve in NW-Zealand as well as on Galgebakke at Næstved (S-Zealand). In both places the soil is fairly rich. The material strongly indicates that with regard to the colour of the perianth *P. pratensis* forms an ecocline from poor to more fertile sandy soils. This result agrees in many respects with the geographical distribution of dark and pale flowering *P. pratensis*. According to VISYULINA (1939) all the material from the Ukrainian SSR with its very fertile steppe soils belongs to *nigricans*, while according to JUZEPČUK both types occur in N. Russia. Of particular interest is the distribution in the Poznan district of Poland (KRAWIEC, 1932). Southern



Table 1. Variation in the colour of the perianth of *Pulsatilla pratensis*.  
(Material from 1933-1935).

Locality	Soil		Number of plants	Colour of perianth, distribution in per cent				
	pH	Type of soil		White	Reddish	Pale violet	Dark or blackish violet	Blackish violet
Tissö .....	7.3	Diluvial sand	50	0.0	0.0	2.0	98.0	68.0
Nissebakker .....	—	“ “	115	0.9	0.0	10.4	88.7	—
Skåneshøj. ....	—	“ “	30	0.0	0.0	11.6	88.4	—
Kregme 1 .....	7.5-8.0	“ “	61	0.0	0.0	14.8	85.2	44.2
Refsnæs. ....	7.6-7.8	“ “	50	0.0	0.0	22.0	78.0	40.0
Frederikssund .....	7.5	“ “	76	0.0	0.0	25.0	75.0	—
Osen .....	—	Alluvial sand	50	0.0	0.0	28.0	72.0	30.0
Frederiksværk .....	—	Diluvial sand	100	0.0	1.0	32.0	67.0	37.0
Køge Ås .....	—	“ “	25	0.0	0.0	40.0	60.0	32.0
Gilleleje 1 .....	5.0	Alluvial sand	83	1.2	2.4	47.0	49.4	—
— 1 .....	5.0	“ “	106	0.0	1.9	56.5	41.6	22.2
— 2 .....	5.2	“ “	100	0.0	0.0	58.0	42.0	22.0
Korshage 1 .....	5.6	“ “	88	0.0	0.0	60.2	39.8	12.5
Kassemose .....	—	Drift sand	100	0.0	4.0	63.0	33.0	24.0
Gilleleje 3 .....	4.9	Alluvial sand	58	0.0	0.0	72.4	27.6	12.1
Jutland N. Tranders. .		Diluvial sand	149	0.0	0.0	28.9	71.1	18.8

populations are pure or almost pure *nigricans* and the northernmost populations pure *pratensis* or a mixture of the two races including plants with intermediate characters. Most of the 19 populations are from the margin of pine woods. It would therefore appear as if a topocline from south to north might exist, but also in this case the cline may be an ecocline. The pure or almost pure *pratensis* populations in the north seem to occur on poor fluvioglacial sands in the surroundings of Bydgoszcz, while the *nigricans* populations east and southwest of Poznań grow on mediocre sandy or podsolated soils (cf. Mały Atlas Polski, map 9, 1947). The correlation between dark flowers and more fertile sands is difficult to explain, but it may be due to some important physiological properties which are linked together with the characters involving dark or light perianth colour. Some observations indicate pale flowering plants to be a little earlier than the dark flowering ones (see e. g. the material from Heather hill and Gilleleje in Table 2).

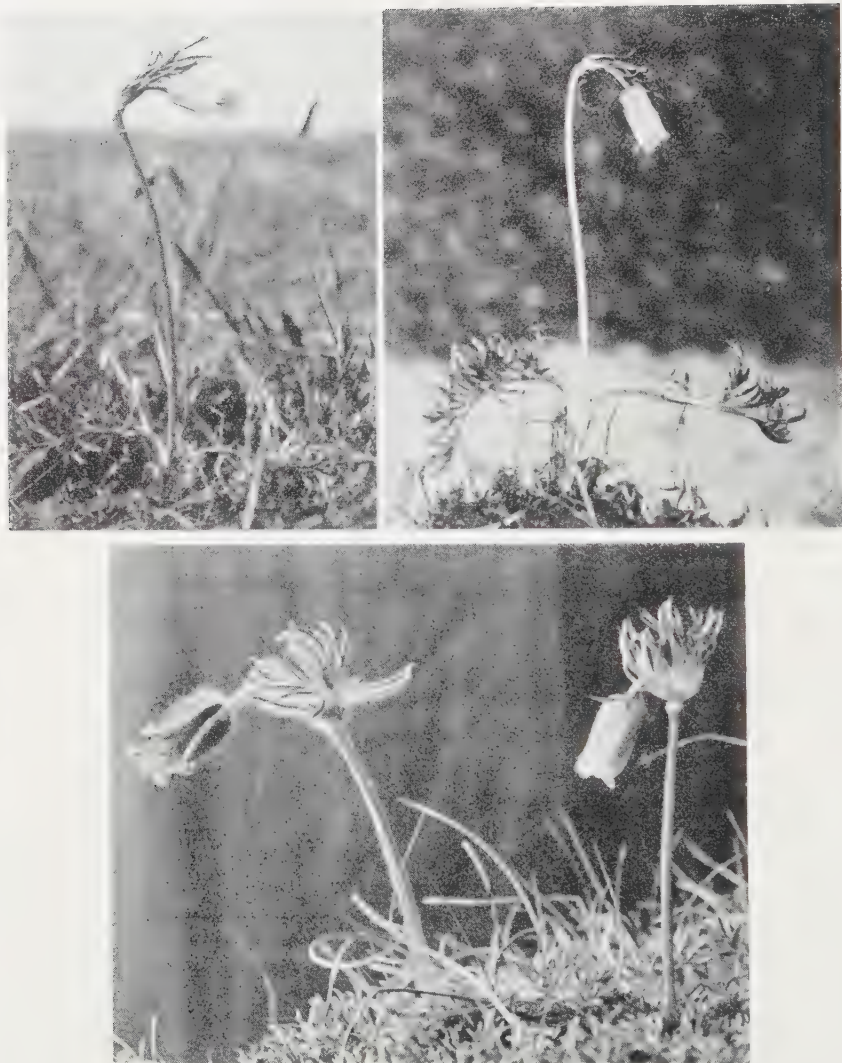


Fig. 1. *Pulsatilla pratensis* f. *johanssonii* HYL. from the Gilleleje 1 population. The specimen in the two pictures above was found in 1932 and had crumpled involucral leaves. The specimen found in 1934 is seen below together with a normal plant with pale violet, long perianth leaves.

The main variation runs from blackish to very pale violet. Some of the darkest flowers, however, are sometimes bluish-violet and some of the light colours may be classified as purplish-violet, pale-purplish or even reddish inclining slightly to tawny. In some cases the perianth leaves

Table 2. Variation in the colour of the perianth of *Pulsatilla pratensis*.  
(Material from 1954).

Locality	Date	Soil		Num- ber of plants	Colour of perianth, distribution in per cent										
		pH	Type of soil		White	Very pale violet green- ish yellow	Red- dish	Pale purpl- ish	Purpl- ish violet	Violet			Dark bluish violet	Dark or blackish	
										Very pale	Pale	Dark			
Hestebjerg at Lejre . . . .		7.0	Diluvial sand	85	0.0	0.0	0.0	0.0	0.0	3.5	3.5	27.1	62.4	3.5	93.0
Kregme 2 . . . . .		7.5	" "	87	0.0	0.0	0.0	0.0	1.2	2.3	10.3	48.2	36.8	1.2	86.2
Bøgebjerg at Rye . . . . .		5.6	" "	100	0.0	0.0	0.0	0.0	1.0	3.0	15.0	49.0	32.0	0.0	81.0
Korsbage 2 . . . . .		6.0	Alluvial sand	117	0.0	1.7	0.0	0.0	10.3	12.0	18.8	43.5	12.0	1.7	57.2
Arreso . . . . .		-	Diluvial sand	64	0.0	0.0	0.0	0.0	0.0	17.2	28.1	35.9	17.2	1.6	54.7
Tibirke Bakker . . . . .		-	Drift sand	82	0.0	0.0	2.4	0.0	0.0	7.3	37.8	35.4	17.1	0.0	52.5
Smidstrup . . . . .		5.7	Alluvial sand	70	0.0	0.0	0.0	0.0	2.9	5.7	40.0	40.0	11.4	0.0	51.4
Skredbjerg at Nakke . . . .		5.0	" "	115	1.7	3.5	0.0	1.7	3.5	16.5	26.1	38.2	6.9	0.9	46.0
Melby Overdrev . . . . .		5.0	Drift sand	71	0.0	0.0	0.0	0.0	2.9	2.9	48.6	25.7	20.0	0.0	45.7
Villingerød . . . . .		5.1	Diluvial sand	50	0.0	0.0	0.0	0.0	0.0	16.0	22.0	30.0	12.0	0.0	42.0
Heather hill at Rågeleje	14.5	5.8	" "	122	0.0	0.0	1.6	0.0	0.0	13.1	30.3	34.4	20.5	0.0	54.9
Heather hill at Rågeleje	27.5	5.8	" "	163	0.0	0.7	0.0	1.8	5.0	10.4	23.9	32.5	23.9	1.8	58.2
Gilleleje 1 . . . . .	14.5	5.0	Alluvial sand	160	0.0	0.0	0.6	0.0	0.0	7.5	51.9	26.3	13.7	0.0	40.0
Gilleleje 1 . . . . .	27.5	5.0	" "	161	0.0	0.0	0.0	0.0	0.0	6.6	34.4	44.2	8.2	0.0	52.4



Fig. 2. *Pulsatilla pratensis*. Two plants found in the Gilleleje 1 population 25th April 1934. To the left a form with very thin pubescence and dark violet flowers. To the right a pubescent albino.

were very pale violet at the tips and pale greenish-yellow at the base (Table 2). This form may be related to that described from Sweden by THEDENIUS (1889) as var. *flava* with yellow, at the base greenish flowers.

The most deviating and rare type is that which HYLANDER (1945, p. 169) called f. *johanssonii*. It is light green with white flowers and lacks hairs. It has been found in Sweden (Gotland and Öland) and was found in 1932 and 1934 by me at Gilleleje in N. Zealand, see Fig. 1, and in 1953 at Korshage in Odsherred (NW-Zealand) by my wife. In all three cases only a single specimen was observed. White flowering and hairy plants have also been found (Nissebakker (Table 1), Skredbjerg in Odsherred (Table 2), and at Gilleleje, see Fig. 2). They mostly occurred as solitary plants. Both types of albinos are probably spontaneous mutants or segregants after crossings between normal plants and such mutants. They were frequently more or less weak and in one case the quite glabrous plants had crumpled and somewhat deformed involucral leaves (Fig. 1). A similar glabrous albino mutant was recently found by ZIMMERMANN, WOERNLE & WARTH (1953) among plants raised from seeds of *P. slavica* var. *rhodopea*.

### 3. Pubescence.

The majority of plants of both species are silky-villous and have long hairy styles. The glabrous f. *johanssonii* described above deviates considerably, forming one extreme in the variation. An intermediate position



Fig. 3. *P. pratensis*, ripe achenes with styles. Nos. 1–2 are normal plants with feathery styles; No. 3 deviating form with very thin pubescence; No. 4 glabrous form (*f. johanssonii*). The colour of the style is slight tawny in No. 4, light brown in No. 1, brown in No. 2 (both with pale violet flowers), and dark chestnut in No. 3 (with dark violet flowers). All from the Gilleleje 1 population.  $\times 2$ .

is held by a form that occurred solitarily in the same population at Gilleleje which contained two individuals of *f. johanssonii*. The plant in question had a very thin cover of soft hairs and dark violet flowers (Fig. 2), what is more interesting, however, is its hairiness on the style. As distinct from normal plants (Fig. 3; 1–2) the hairs on the styles were very short and scattered (Fig. 3; 3). The achenes also carried some very short hairs in their upper parts. Normal plants may have achenes which are either entirely covered by hairs or glabrous at the base (Fig. 3; 1–2).

#### 4. Number, Size, and Form of Perianth Leaves; Double-flowering; Occurrence of Plants with two Flowers on the same Stem.

In *P. vulgaris* the number of perianth leaves varied between 5 and 9 (5 leaves: 5.4 per cent; 6 leaves: 66.2 per cent; 7 leaves: 17.5 per cent; 8 leaves: 9.5 per cent; 9 leaves: 1.4 per cent). In *P. pratensis* there were between 5 and 8 leaves (5: 2.6 per cent; 6: 94.1 per cent; 7: 2.6 per cent; and 8: 0.7 per cent). In the population at Rågeleje ("Heather hill", Table 2) a few plants had 7–10 perianth leaves and looked very strange, the outermost leaves being lacinate, consisting of a number of narrow lobes and, apart from colour and size, resembling involucre leaves,





Fig. 4. *Pulsatilla vulgaris*. Villingeröd population in May 14th 1954. Three flowering specimens with narrow perianth leaves.

while the inner perianth leaves were sometimes tripartite with a broad middle lobe (Fig. 5 left). In *P. vulgaris* the same type of divergence was described by ZIMMERMANN (1934, p. 210); it was also seen in a few plants in the Zealand population at Villingeröd.

The last-mentioned population of *P. vulgaris* also contained a number of greatly deviating plants with 6–7 narrow oblong perianth leaves. Whereas the length divided by the breadth of normal perianth leaves was between 2.2 and 3.0, this proportion in the deviating plants was between 4.3 and 5.0 (see Fig. 4) and between 3.0 and 4.3 in flowers on intermediate plants. One specimen had three short outer and three long inner perianth leaves and similar plants with the outer leaves curved backwards were rather common in *P. pratensis*.

In some of the populations of *P. pratensis* there was a slight correlation between dark-violet perianth colour and perianth leaves which exceed the stamens (stamens  $\frac{1}{4}$ – $\frac{1}{3}$  shorter than the perianth). In other populations, however, no such correlation existed and in one population with a majority of pale flowers most of these had leaves which were longer than the stamens. Thus, the proportion between the length of the perianth leaves and that of the stamens cannot be used as a basis for a separation of two species (cf. the descriptions of *P. pratensis* and *P. nigricans*).

The *P. vulgaris* population at Villingeröd contained a number of



Fig. 5. *Pulsatilla pratensis*. Heather hill population 14th and 27th of May 1954. To the left specimen with lacinate perianth, to the right double flowering specimen with four flowers two of which are withering and now only with a few silky leaves on the surface of the receptacle. The normal perianth, the spreading petaloid stamens and the silky leaves replacing the achenes are seen on the flower in side view.

plants which deviated conspicuously by having green silky and (at the top) tripartite leaves instead of carpels. The plants generally had a normal perianth and the outer stamens also looked normal, but on the point of transition from stamens to the leafy carpels some very peculiar stamens occurred. They all had a filament; some of them had an anther which was densely silky; in other cases the filament continued in a short leafy and silky connective which sometimes had only one lateral, somewhat curved locule. In the Heather hill population of *P. pratensis* there was a single double-flowering plant also with a normal perianth, but in this case all stamens were dark violet and petaloid although very narrow (hardly 1 mm broad, see Fig. 5). Again the carpels were replaced by silky leaves, very narrow at the base but with three and five narrow lobes at the top. Thus, in both cases of double-flowering a morphological distinc-

tion exists between stamens and carpels and in both cases the carpels are transformed into leaves which resemble small vegetative leaves. Double-flowering in *P. vulgaris* was also briefly mentioned by ZIMMERMANN (1934, p. 214).

Plants of *P. pratensis* with one additional, mostly small, flower on the same stem are not very rare; they were observed at Gilleleje and Rörvig on several excursions, occurring solitarily between normal plants. Corresponding deviating plants of *P. vulgaris* were mentioned by ZIMMERMANN (1934, p. 202).

### 5. Rosette Leaves.

The Villingeröd population of *P. vulgaris* has narrow leaf segments and belongs clearly to the western ssp. *germanica*. Also in *P. pratensis* the segments are narrow, but the variation in the breadth of segments is greater (from 1–3 and, rarely, up to 5 mm). No correlation between dark flowers and narrow segments could be demonstrated, but a slight correlation of this kind is not improbable and ought, to be studied more closely. The study in natural populations is impeded by the fact that the breadth of the segments and the segmentation itself is influenced by the environment. In some of the populations of *P. pratensis* (much less pronounced in the population of *P. vulgaris*) a number of plants had very broad (up to 10 mm) and frequently comparatively few segments. Such plants have proved to be modifications produced by wounding (picking) or sand-covering. When cultivated, the broad segmented leaves could be produced experimentally by cutting the basal leaf rosettes. The formation of broad segmented leaves may be regarded as a rejuvenation, seeing that juvenile leaves in *P. pratensis* are broad segmented and only tripartite.

### 6. Chromosome Number, Pollen Diameter, and Size of Plants.

Through the studies of LANGLET (1927), BÖCHER (1932), MOFFET (1932), ZIMMERMANN (1932), GUINOCHE (1935), SAKAI (1935), ROSENTHAL (1936), and GREGORY (1941) a polyploid series has been demonstrated in the genus *Pulsatilla* comprising the chromosome numbers  $n = 8, 12, 16,$  and 24.

In *P. pratensis* diploid plants ( $n = 8$ ) have been found in many populations, thus in Denmark at Nibe (BÖCHER, 1932) and Mulbjergene in Jutland as well as at Rörvig, Rågeleje and Refsnæs on Zealand. The





Fig. 6. *Pulsatilla pratensis*, Kregme population 22th May 1936. To the left normal plants, to the right the tetraploid var. *duplex* (type specimen).

diploid number is also found in cultures raised from seeds from Öland, Poland and Hungary (ssp. *hungarica* Soo). In the other species of the *P. pratensis*-complex, *P. montana*, the chromosome number is not constant since races have been demonstrated with 8, 12, 16, and 24 chromosomes (LANGLET, ROSENTHAL, MOFFET, and GUINOCHET loc. cit.).

In the *P. vulgaris*-complex the tetraploid number is prevalent, but according to ROSENTHAL plants of *P. bulgarica* originating from Sofia and very much resembling *P. vulgaris* was diploid. Another diploid strain from wild sources occurred in Yugoslavia; it was sent to me by the Zagreb Botanical Gardens. In culture it deviated mainly in the blackish violet colour of the perianth and the early flowering.

In the populations of *P. pratensis* Gilleleje 1, Kregme, Osen, Skåneshøj, Rågeleje (Tables 1–2) as well as at Höve single plants were found which were very large. Some of these, which had a stem diameter of 4.5 mm (normal plants have stems with a diameter of 2–3 mm, see below) but not very large flowers, proved to be diploids; others, with up to 5–6 mm thick stems and flowers which at the base were 20 mm in diameter (normal plants have a flower diameter of 12–16 mm) were tetraploid or probably tetraploid.  $2n = 32$  was demonstrated in the material from Kregme (Fig. 6) in mitosis in the styles and made very probable for the Höve material through investigations of the pollen size which corresponded to that found in the tetraploid plant from Kregme. As the tetraploid giant plants can be recognized through several characters (size of anthers, breadth of involucral leaves, diameter of stem, flower and pollen grains) it seems natural to describe them as a special variety:

*Pulsatilla pratensis* (L.) MILL. var. *duplex* nov. var.

A var. *pratensi* differt omnibus partibus majoribus. Diametros caulis 5–6 mm, floris 20 mm. Latitudo laciniarum involucralium 3–5 mm. Longitudo antherae vivae 1.8–2 mm. Diametros pollinis plerumque 38–42  $\mu$ . Numerus chromosomatum  $2n = 32$ .

In populationibus nonnullis Selandicis varietatis *pratensis* (cui numerus chromosomatum  $2n = 16$ ) singillatim occurrit. Typus 22.5.1936 prope Kregme Selandiae borealis lectus, in Museo Botanico Hauniensi depositus.

Measurements of the pollen size are given in Table 3. It will be seen that normal *P. pratensis* plants (including a plant that was found to be diploid) had pollen diameters of between 28 and 35  $\mu$ , rarely more or less, while var. *duplex* had its maximum between 38.5 and 42  $\mu$ . It is interesting to note that a corresponding difference in pollen size was found in diploid and tetraploid *P. vulgaris* in spite of the fact that in this case the diploid was a very tall plant with a thick stem and large flowers. The pollen size in anthers from one of the double-flowered *P. vulgaris* plants was smaller, a fact which may be due to poor nutrition of the pollen grains during their development or to unknown cytological disturbances.

## 7. Relation between *P. pratensis* and *P. vulgaris*.

Both species of *Pulsatilla* occur in the hills at Villingeröd. It is remarkable, however, that they only very rarely grow together, although the communities and the soil where they grow seem to be almost identical. Nevertheless, cross pollination may occur rather frequently, but no hybrids have ever been positively identified. On some of the *P. vulgaris* plants even young flowers nodded almost like *P. pratensis*, but these plants were not intermediate in any other characters and may therefore belong to a special form of *P. vulgaris* (f. *bogenhardiana*, cf. ZIMMERMANN, 1932, pp. 425–426).

Growing side by side it is not difficult to keep the two species apart even in a fruiting stage. The stems of *P. vulgaris* are thicker and, during the flowering, greener than those of *P. pratensis*. The diameter of the stems of *P. vulgaris* varied between 2.5 and 4.5 mm, the stem of *P. pratensis* ranged from 2 to 3 mm, but in other populations of *P. pratensis* normal diploid plants occurred with somewhat thicker stems. The stem diameter, therefore, is not a good distinguishing character. The rigidity of the stem below the involucre is a much better characteristic. In *P. vulgaris* the stem has a wider central hollow and its supporting tissues





are not so well developed as in *P. pratensis*. Consequently the stem of the latter is more rigid. On the whole *P. pratensis* is much more xerophytic with roots frequently reaching 50–90 cm whereas the roots of *P. vulgaris* do not penetrate more than about 20–50 cm into the soil.

JANCZEWSKI (1888–89) crossed *P. pratensis* (with pale-violet flowers) with *P. vulgaris* (as the male plant). In 1886 all the seeds were sterile, but in 1887 few seeds were viable. The hybrid was described as being dominated by the characters of *P. vulgaris*. JANCZEWSKI drew the conclusion that since this hybrid was so very difficult to produce, its occurrence in nature was extremely doubtful. He said that all previous records ought to be regarded as erroneous. JANCZEWSKI's opinion, however, did not prevent ASCHERSON & GRÄBNER (1898–99) from recording the hybrid as occurring in Brandenburg and more recently MEUSEL (1939, p. 187) spoke about "zweifelloser Hybriden" in Kyffhäuser in central Germany.

After the finding of the tetraploid var. *duplex* the possibility has arisen that tetraploid hybrids between this variety and tetraploid *P. vulgaris* are produced occasionally where these plants occur intermixed. In northern Europe where diploid *P. vulgaris* may be missing any interchange of genes between the two species may thus depend on the presence of var. *duplex*.

### Literature.

- ASCHERSON, P. & GRÄBNER, P., 1898–99: Flora des Nordostdeutschen Flachlandes. Berlin.
- BECK, G., 1890: Flora von Nieder-Osterreich I.
- BÖCHER, T. W., 1932: Beiträge zur Zytologie der Gattung Anemone. Bot. Tidsskr. 42: 183–206.
- 1945: Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. II. Dan. Biol. Skrifter 4, 1: 1–159.
- GREGORY, W. C., 1941: Phylogenetic and Cytological Studies in the Ranunculaceae. Trans. Am. Philos. Soc. 31, 5: 443–520.
- GUINOCHE, M., 1934: Contribution à l'étude génétique et cytologique du genre Anemone. Rev. Cyt. et Cytophys. Veget. 1, 131–149.
- v. HAYEK, A., 1904: Kritische Übersicht über die Anemone Arten aus der Sect. Campanaria. Festschr. f. Ascherson. Berlin.
- HYLANDER, N., 1945: Nomenklatorische und systematische Studien über nordische Gefäßpflanzen. Uppsala Universitets Årsskrift 1945, 7: 1–337.
- JALAS, J., 1950: Zur Kausalanalyse der Verbreitung einiger nordischen Os- und Sandpflanzen. Annales Bot. Soc. Zool. Bot. Fennicæ "Vanamo". 24, 1: 1–362.
- JANCZEWSKI, E., 1888–1889: Les Hybrides du genre Anemone I–II. Bull. internat. Acad. Scienc. Cracovie. Comptes rendus des Sciences. Cracovie, pp. 1–24.

- JUZEPČUK, S. V., 1937: Pulsatilla, in KOMAROV & SISKIN: Flora SSSR 7: 301–302. Moskva.
- KOTOV, M., 1940: Description of New Species of Flora of Ukr. SSR. Journ. Bot. Acad. Scienc. de la RSS d'Ukraine 1: 275–279.
- KRAWIEC, F., 1932: Über die Verbreitung der Küchenschelle (Pulsatilla Tourn.) in Grosspolen. Acta Soc. Bot. Polon. 9: 531–537.
- LANGLET, O., 1927: Beiträge zur Zytologie der Ranunculaceen. Svensk Bot. Tidskr. 22: 1–17.
- MEUSEL, H., 1939: Die Vegetationsverhältnisse der Gibbsberge im Kyffhäuser und im südlichen Harzvorland. Hercynia 2: 1–372.
- MOFFET, A. A., 1932: Chromosome studies in Anemone I. Cytologia 4: 26–37.
- OSTENFELD, C. H., 1911: The Distribution within Denmark of the Species of Anemone, Hepatica and Pulsatilla. Biol. Arb. tilegn. Eug. Warming, pp. 241–263. Copenhagen.
- PRITZEL, G. A., 1841: Anemonarum revisio. Linnaea 15, 5 (Halle).
- ROSENTHAL, C., 1936: Chromosomenstudien an Pulsatilla. Jahrb. wiss. Bot. 83: 809–844.
- SAKAI, K., 1935: Studies on the Chromosome Numbers in Alpine Plants. Jap. Journ. Genet. 11: 68–73.
- THEDENIUS, C. G. H., 1889: Några egendomliga fanerogamformer från Åhus i Skåne. Bot. Notiser 1889: 68–70.
- WANSCHER, J. H., 1953: Forenklede beskrivelser af blomsterfarver. Årbog for Gartneri 1952.
- VISYULINA, E., 1939: On the Taxonomy of the Genus Pulsatilla in the Flora of the Ukrainian SSR. Journ. Inst. Bot. Acad. Scienc. de la RSS d. Ukraine. No. 21–22 (29–30): 257–266.
- ZÄMELS, A. & PAEGLE, B., 1927: Untersuchungen über den anatomischen Bau der Blattstiele in der Gattung Pulsatilla Tourn. Acta Horti Bot. Univ. Latv. 2: 133–161.
- ZIMMERMANN, W., 1932: Beiträge zur Kenntnis der Georeaktionen IV, Jahrb. wiss. Bot. 77: 393–506.
- 1934: Genetische Untersuchungen an Pulsatilla I–III. Flora 129: 158–234.
- 1939: Genetische Untersuchungen an Pulsatilla IV. Flora 133: 417–492.
- ZIMMERMANN, W., WOERNLE, D. & WARTH, L., 1953: Genetische Untersuchungen an Pulsatilla V. Zeitschr. f. Bot. 41: 227–246.

## Two New Species of *Laurencia* from Mauritius

By F. BÖRGESEN

In a collection of algae recently received from Mauritius one of the gatherings, upon examination, appeared to contain two small *Laurencia* species. At a first glance they seemed to be much alike as to the shape and size but, after a somewhat closer examination, they nevertheless turned out to be very deviating and, as I think, each to be the representative of a new species.

### *Laurencia subcolumnaris* nov. spec.

*Thallus cartilagineus, caespitosus, laevis, ex partibus decumbentibus et partibus erectis compositus. Frondes erectae subcylindrico-claviformes, ca. 1–1.5 cm. altae, simplices aut ramosae, ramis subclavatis 1–5nis in partibus superioribus frondium ortis, apicibus late rotundatis.*

*Cellulae superficiales thalli parietibus ca. 10  $\mu$  crassis extrorsum tectae, radiatim elongatae, ca. 30  $\mu$  longae et 12–15  $\mu$  latae, ad apices thalli versus latiores, subquadratae. Cellulae medullares extrorsum parvae, ad medium versus majores, ca. 120  $\mu$  latae.*

*Tetrasporangia in apicibus thalli formata, ca. 100  $\mu$  lata. Antheridia et cystocarpia ibidem.*

*Mauritius: Pointe aux Roches, 22.9.52. G. MORIN no. 1286 (pro parte).*

Upon exposed rocks this little *Laurencia* (Fig. 1) forms small tufts composed of subcylindrical-clavate erect filaments issuing from quite short decumbent filaments, more or less merging into irregularly shaped discs firmly fastened to the substratum.

The largest specimens I have seen are up to about 1.5 cm. high. A good many of the erect filaments seem to remain unbranched; the terete, subclavate, stem-like filaments are about 0.5 mm. broad near the base.

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<sup>1)</sup> I am much indebted to Cand. mag. TYGE CHRISTENSEN for his valuable help with the Latin diagnoses and the photographs and to Stud. polyt. JENS TH. KEIDING for help with the drawings.



Fig. 1. *Laurencia subcolumnaris* nov. spec. Some dried specimens. ( $\times 1$ ).

slowly increasing in size upwards to about 1 mm., and above they end in the broadly rounded apex with the pit in the middle. But most of the specimens are divided (Fig. 2), issuing a single or up to 5–6 branches somewhat below their summits; the branches become thicker upwards, getting a clavate appearance.

As to the anatomy (Fig. 3), the surface cells in the lower part of the thallus are palisade-like, about twice as long as broad (about  $30\mu$  long and  $15\mu$  broad), and covered by a very thick epidermal layer about  $10\mu$  thick or more. In the upper part of the thallus the surface cells gradually become a little broader, more subrectangular, and the surface layer a little thinner.

Near the periphery the medulla consists of small, roundish cells becoming rapidly larger towards the middle; the central cells are about  $100\text{--}120\mu$  in diameter. A longitudinal section shows that the cells of the medulla increase in length towards the middle of the thallus up to about  $200\text{--}300\mu$ .

Tetrasporic as well as antheridial and cystocarpic specimens are found.

The tetrasporangia are developed at the upper end of the specimens and often in rather regular rows (about eight), radiating from the apex downwards along the periphery of the thallus. The sporangia are globular, tetrahedrally divided, rather large, with a diameter of about  $100\mu$  and provided with a wall about  $10\mu$  thick.

A single small antheridial cave has been observed in the wall a little below the apex of a specimen, and some few cystocarps of the usual obovate shape have been observed near the summit of the specimen.

As to the size and habit this little species must be said to be very alike *Laurencia humilis* SETCHELL and GARDNER, described in their paper: "Marine Algae of the Revillagigedo Islands Expedition in 1925". (Proceed. of the California Academy of Science, fourth Series, vol. XIX, no. 11, Dec. 30, 1930). But when the structure of the two species are





Fig. 2. *Laurencia subcolumnaris* nov. spec. A specimen with tetrasporangia. ( $\times 10$ ).

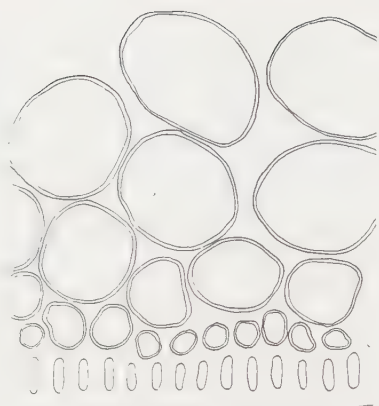


Fig. 3. *Laurencia subcolumnaris* nov. spec. Transverse section of the thallus. ( $\times$  ca. 150).

compared essential differences are found. Thus the surface cells in the Mauritian plant are palisade like with very thick walls while these in *Laurencia humilis* are quite variable in shape and size, mainly sub-circular in surface view, up to  $30\ \mu$  diam. And while the chromatophores are small and lobed in *L. subcolumnaris* those in *L. humilis* forms a network of crooked rods. And while the sporangia in the Mauritius species are in most cases nicely arranged in about eight rows, issuing from the apex downwards in the upper part of the thallus, those in *L. humilis* are "crowded at the outer ends of the filaments".

#### *Laurencia verruculosa* nov. spec.

*Thallus cartilagineus, caespitosus, superficie verruculosus. Ramuli decumbentes rhizoidibus brevibus ad saxa adfixi. Frondes erectae ad 1.5–2 cm. altae, subcylindricae, repetite furcatae, ad bases ca. 0.50 mm. crassae, ad apices versus sensim ad 0.75 mm. incrassatae.*

*Cellulae superficiales thalli subcylindricae, ca. 60–70  $\mu$  longae et 20–30  $\mu$  latae, parietibus 3–7  $\mu$  crassis, extrorsum in tholos productis, superficiem ita verruculosam reddentibus. Cellulae medullares rotundatae, parietibus crassis, extrorsum minores, ad medium versus paululum majores. Organa fructifera non observata.*

*Mauritius: Pointe aux Roches, 22.9.52. G. MORIN no. 1286 (pro parte).*

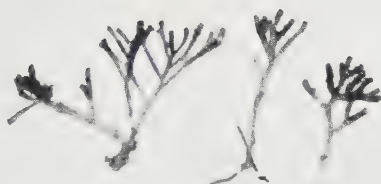


Fig. 4. *Laurencia verruculosa* nov. spec. ( $\times 1$ ).

Mixed with the small *Laurencia* mentioned above there was another species of this genus, rather similar as to shape and size (Fig. 4). After a somewhat more thorough examination it was, however, found to differ very essentially from the species mentioned above.

The most conspicuous difference is that the plant, when observed even at slight magnification, is found to have a very strongly dotted surface. At higher magnification it appears that this is due to the fact that the upper ends of each of the very thick-walled, palisade-like surface cells are provided with a large dome-like excrescence<sup>1)</sup> (Fig. 5).

As to the habit of this species (Fig. 4), when compared with the one mentioned above, it is a little slenderer and more branched, the branches issuing from lower down on the thallus and becoming ramified again.

The branches are given out at acute angles. The largest specimens found have a height of about 1.5 cm.; according to the few specimens I have seen the plant forms small tufts.

The base of the plant consists of irregularly shaped, decumbent filaments from which rhizoids are given out which fix the plants firmly to the rocks.

As said above, the surface cells are palisade-like and elongate, and in transverse sections (Fig. 5) it is seen that their walls are about  $5-7\mu$  or more in thickness, and their apical semiglobular free ends are about  $10-15\mu$  high. The rather narrow lumen of the cells is of variable size,

<sup>1)</sup> In Mar. Alg. D. W. I., vol. II, part 4, p. 247, fig. 235 I have pictured a small part of a transverse section of a *Laurencia* referred to *L. Poitei*, the surface cells of which had some similar, but much smaller excrescences.

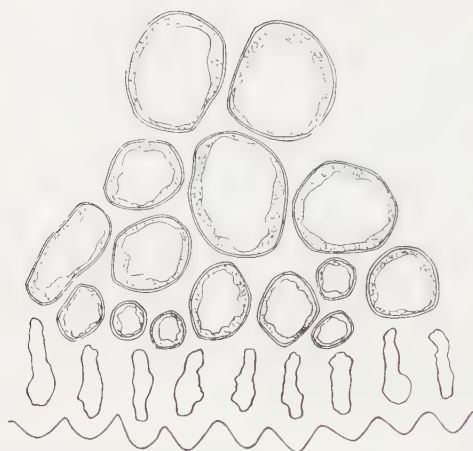


Fig. 5. *Laurencia verruculosa* nov. spec. Transverse section of thallus. ( $\times$  ca. 150).

down to  $5-6\mu$  broad and  $30-40\mu$  long; the epidermal layer upon the whole is about  $60-70\mu$  or a little more thick.

A cross section of the medulla shows that it consists of small roundish cells becoming somewhat larger inwards, but on the whole small, having a diameter of about  $60-70$ , up to about  $100\mu$ , rarely more. The walls of the cells have rather expanded but not very broad thickenings. Upon longitudinal section it is found that the cells of the medulla are sub-cylindrical, about  $200-300\mu$  long.

The specimens are sterile.

The locality for both species is described like this: "On rocks exposed to strong surf."

According to the above description of the shape and structure of these two small *Laurenciae* and taking into consideration the description of the locality, I presume that they, felted together as they are, have formed low, more or less dense, firm tufts upon rocks, being in that way very able to resist not only the strong surf, but also during ebb-tide the peril of being dried up.

## Some Considerations on the Phylogeny of the *Bryophyta*

By TYGE CHRISTENSEN

For many years the question of the origin of the *Bryophyta* has been connected with that of the origin of the heteromorphic alternation found in all archegoniate plants. Most botanists have held that the *Bryophyta* and the *Pteridophyta* have a common origin from haplontic green algae, and the central subject of discussion has been the alternative explications possible as to the origin of the diploid phase: (1) The sporophyte developed gradually de novo by the zygote undergoing an increasing number of mitotic divisions before meiosis. In this case—intercalation of the sporophyte—the first *Bryophyta* in evolution must have had a very simple sporophyte, consisting of little more than the sporogenous tissue. (2) The diploid sporophyte arose at one step by a postponement of meiosis from the germination of the zygote to the next formation of spores. In this case—transference of meiosis—the first haplodiploids in the ancestry of *Bryophyta* must have been isomorphic like such green algae as *Ulva*, and the first plants referable to the *Bryophyta* must have had sporophytes that were relatively independent of the gametophytes.

ZIMMERMANN (1930 and 1932) collected the various arguments for either theory and found them almost equal, with a slight preponderance in favour of transference of meiosis. More have argued for the latter since then, but the intercalation hypothesis still holds a strong position. It gives a straight line of evolution from the most primitive *Bryophyta* through the *Pteridophyta* up to the *Spermatophyta*, and the simplicity of such progression may be partly responsible for the fact that considerable difficulties in accepting today the intercalation hypothesis are rather disregarded.

First, our present knowledge of life cycles in other groups of plants definitely goes against intercalation as the process leading to haplodiploidy

in the *Archegoniatae*. Isomorphic alternation is found both in red, brown and green algae and must either be a very primitive type of cycle found in the ancestors common to these three groups, such as supposed by FELDMANN (1952), or must have arisen independently at three or more different occasions by a transference of meiosis, such as supposed by FRITSCH (1942). Heteromorphic alternation, on the other hand, is found only in such groups of algae where a derivation from an isomorphic cycle is nearly beyond doubt. The sole exception is that of the Floridean carposporophyte, which has a much simpler structure than the corresponding gametophyte and tetrasporophyte. For this FRITSCH l. c. presumes an intercalation to have taken place, while FELDMANN advocates a derivation from an isomorphic form as in all other cases. However this may be, no evidence is found in any algal group, and very little probability as to the green algae—whose life cycles are of major interest in connexion with the phylogeny of the *Bryophyta*—that a diploid generation ever arose by intercalation.

A second objection to the theory of intercalation, as being applied to the whole of the *Archegoniatae*, is afforded by the parasitism of the Bryophyte sporophyte. The idea that fully autotrophic plants should be derived from parasites, contrasts strongly with what is thought to be the normal pattern of evolution (cp. the so-called DOLLO's Law). It seems impossible, for instance, that the gametophyte of flowering plants should ever in future give rise to a plant with all functions necessary for a physiologically independent life. The same must apply to the *Bryophyta*, thus making it little probable that a sporophyte which parasitised on the gametophyte for the whole of its life should develop into the autotrophic sporophyte of the *Pteridophyta*. On the other hand, a Bryophyte evolution in the opposite direction—towards increasing parasitism and neoteny—will correspond to what is supposed to have taken place in vascular plants as well as in other groups of plants, and does not give any offence to thought. So for this reason as well, one must support the view that the ancestors of Bryophytes had an isomorphic alternation.

These considerations point in the same direction as the discovery by HOLLOWAY (1939) that in some cases (cp. MANTON, 1942 and 1950) *Psilotum* is provided with tracheides in the gametophyte as well as the sporophyte, thus showing a lower degree of heteromorphism than hitherto known in the *Cormophyta*. Altogether the evidence seems so strongly in favour of an isomorphic alternation in the ancestry of all archegoniate plants that the interpolation hypothesis should at last be totally abandoned.



This being accepted, a small step further can be taken: The group of plants denoted as *Pteridophyta* is morphologically very heterogeneous, comprising—if maintained as a systematic unit at all—so different types as the ferns, the horsetails and the thalloid *Psilophytinae*. In fact, the *Pteridophyta* are defined only as *Archegoniatae* with sporophytes independent of the gametophytes at the time of spore formation. This definition involves that the ancestral form of the *Archegoniatae* can be placed with considerable probability among the *Pteridophyta* even without being known, simply on account of the fact that it has given rise to forms with autotrophic sporophytes.<sup>1)</sup>

After this the transitional type must be asked for: What did that unknown plant look like whose sporophyte became first a full life parasite on the gametophyte? To this question a formal answer can be given: The hypothetic plant possessed all such morphological features as are found both in the *Bryophyta* and the *Pteridophyta*, provided that these features are homologous in the two groups.

CHADEFAUD (1950) presumes that *Bryophyta* and *Pteridophyta* should be derived from a common, nearly isomorphic type with both gametophyte and sporophyte consisting of leaf-bearing stems more or less similar in structure to the recent *Tmesipteris*. He imagines this hypothetic form as having the sporophytes borne on the gametophytes, and supposes that the type of the recent *Pteridophyta* arose by a reduction of the gametophyte, bringing about that the sporophyte was implanted in the soil. For the reason mentioned above it seems much more probable that the sporophyte of the *Pteridophyta* was primarily autotrophic, such as supposed by FRITSCH (1945). Such opinion does not, however, prevent acceptance of CHADEFAUD's hypothetic form as an ancestor of the *Bryophyta*; only it should be derived itself from forms with autotrophic sporophytes. The acceptance involves that the primitive Bryophyte leaf must be regarded as homologous with the leaf of at least some *Pteridophyta*. On this point CHADEFAUD has later (1952) expressed some reservation himself, without entering again on the question of phylogeny. If the assumption holds true, that the gametophyte of the first Bryophytes had a leafy stem, the leafless stem or simple thallus found in some recent forms must in all cases have arisen by reduction.

<sup>1)</sup> Such connexion is listed by ZIMMERMANN (1930) as one of the derivations possible, and is said to be advocated by CAMPBELL (1905 and 1925). CAMPBELL's papers, however, speak in definite terms for interpolation. The conclusions to be drawn from LANG's ideas (1909) are more similar, while a precise formulation is given by SCOTT (1929).

The question of homology also rises with regard to the sporangium. That found in the Devonian and late Silurian *Rhyniaceae* and in some of the contemporary leaf-bearing plants has been repeatedly compared with that of the *Anthoceroles*, both being terminal and both being provided with a columella in some genera. An absolutely doubtless homology cannot be ascertained, since the type of sporangium in question is relatively simple, and may have arisen twice in evolution; but an independent origin in the two cases seems little probable in view of the difficulties involved in connecting even this "simple" type of sporangium with such sporangia as are found in present-day *Chlorophyta*.

A third similarity between vascular plants and some *Bryophyta* should be adduced as being most likely due to true homology: The structures termed root-hairs in the gametophytes and sporophytes of vascular plants are quite identical with those termed rhizoids in the *Anthoceroles* and the *Hepaticae*—both being tubular unseptate outgrowths from superficial cells—but fundamentally different from the secondary protonema termed rhizoids in the *Musci*. The acceptance of a homology in this case means that forms to be grouped together with the recent *Musci* must be excluded as possible ancestral types.

Furthermore, all forms with such reduced, quite or nearly colourless sporophytes as found in the recent *Hepaticae* must be excluded as ancestors of *Bryophyta* with green sporophytes.

In consequence, the first *Bryophyta* in evolution must either have been rather similar to the *Anthoceroles* of today, or to none at all of the recent groups.—Three major possibilities exist:

(1) The *Bryophyta* are to be derived from *Pteridophyta* with leaves on the stem of the gametophyte as well as that of the sporophyte. Evolution has then led from these *Pteridophyta* to primitive *Bryophyta* which must be imagined as having sporophytes similar to those of the recent *Anthoceroles*, borne on gametophytes more or less like those of recent *Bryales*, though with rhizoids like those of the *Anthoceroles* and the *Hepaticae*.

(2) The *Bryophyta* are to be derived from such leafless *Pteridophyta* as the *Rhyniaceae*. Some of these extinct forms are in fact so easily connected with some of the recent *Anthoceroles* that a shorter transition can hardly be imagined for a formerly autotrophic sporophyte to become a parasite on the gametophyte and at the same time neotenic, combining reproductive maturity with a juvenile stage of vegetative development. This is the derivation proposed by SCOTT (1929) and supported by HASKELL (1949) and TAKHTAJAN (1950 and 1953). It involves that the various *Bryophyte*

leaves are not homologous with the leaves of any vascular plants, and possibly not mutually, either.

(3) The *Bryophyta* are to be derived polyphyletically from different types of *Pteridophyta*, some from leaf-bearing forms, others from the—primarily or secondarily (cp. MARTENS 1950)—leafless *Rhyniaceae* or types similar to these.

In any case heteromorphism must be supposed to have been little advanced at the outspring of *Bryophyta*. The agent that led the sporophyte to develop perched on top of the gametophyte may have been the same as indicated by FRITSCH (1945) as an explication to the proceeding heteromorphism in vascular plants: The asexual spores should be produced as high up as possible in order to be well spread by the wind, while the archegonia and antheridia should develop near to the ground because of the necessity of water for fertilisation.

No matter how the phylogenetical lines should be drawn in detail, the fact must be accepted that biochemical research as well as investigations into the flagellar structure has today removed the last traces of doubt as to the evolutionary connexion from the *Archegoniatae* back to green algae. In zoology the realisation of a similar situation of the "higher animals" has resulted in a systematic rearrangement long ago. For instance CLAUS, GROBBEN and KÜHN (1932) have no less than four taxa of higher rank above that of the *Vertebrata*. An inclusion of *Bryophyta* and vascular plants among the *Chlorophyta* would be a natural parallel in botany.

### Literature.

- CAMPBELL, D. H., 1905: The Structure and Development of Mosses and Ferns. 2. ed. New York.
- 1925: The relationship of the Anthocerotaceae. *Flora. N. F.* 18–19 Goebel-Festschrift: 62–74.
- CHAUDEFAUD, M., 1950: Les Psilotinées et l'évolution des Archegoniates. *Bull. Soc. Bot. France* 97: 99–100.
- 1952: La leçon des Algues. *Colloque Intern. Évol. et Phylog.* 9–23. *L'Année Biologique*. 3. sér. 28.
- CLAUS, C., GROBBEN, K. und KÜHN, A., 1932: *Lehrbuch der Zoologie*. 10. Aufl.
- FELDMANN, J., 1952: Les cycles de reproduction des Algues et leurs rapports avec la phylogénie. *Rev. Cytol. et Biol. Végétales*. 13: 1–49.
- FRITSCH, F. E., 1942: Studies in the Comparative Morphology of the Algae. II. The Algal Life-Cycle. *Annals of Bot. N. S.* 6: 533–563.
- 1945: Studies in the Comparative Morphology of the Algae. IV. Algae and Archegoniate Plants. *Ibid.* 9: 1–29.

- HASKELL, G., 1949: Some Evolutionary Problems concerning the Bryophyta. *The Bryologist* 52: 49–57.
- HOLLOWAY, J., 1939: The Gametophyte, Embryo and Young Rhizome of *Psilotum triquetrum* Swartz. *Annals of Bot. N. S.* 3: 313–336. With pl. VIII–IX.
- LANG, W. H., 1909a: A theory of Alternation of generations in the Archegoniate plants based upon the Ontogeny. *New Phytol.* 8: 1–12.
- 1909b: Discussion on “Alternation of Generations” at the Linnean Society. *Ibid.* 104–116.
- MANTON, I., 1942: A Note on the Cytology of *Psilotum* with Special Reference to Vascular Prothalli from Rangitoto Island. *Annals of Bot. N. S.* 6: 283–292. With pl. VIII.
- 1950: Problems of Cytology and Evolution in the Pteridophyta. Cambridge.
- MARTENS, P., 1950: Le caractère “aphylle” des Rhyniales est-il primitif? *Bull. Classe Sciences Acad. Royale Belg.* 5<sup>e</sup> Sér. 36: 811–822.
- SCOTT, D. H., 1929: Aspect of Fossil Botany. II. Early Floras. *Nature* 123: 350–352.
- TAKHTAJAN, A. L., 1950 and 1953: Phylogenetic Principles of the System of Higher Plants. *The Bot. Review.* 19: 1–45, 1953: transl. from *Botanicheskii Zhurnal* 35, 1950.
- ZIMMERMANN, W., 1930: Die Phylogenie der Pflanzen. Jena.
- 1932: Phylogenie. 433–464 in F. Verdoorn: *Manual of Bryology*. The Hague.

## *Nanostictis*, a New Genus of Scolecosporous Discomycetes

By M. SKYTTE CHRISTIANSEN

A very small discomycete was found growing on the thallus of *Peltigera polydactyla*. The character of its asci and its filiform spores refer it to the order *Ostropales* NANNFELDT (1932), where it is believed to constitute the type of a new genus, described below sub nom. *Nanostictis*. Its relation to the other genera of this order is discussed. The structure of excipulum in *Stictis radiata* (L.) PERS. is studied more closely in order to illustrate the differences between the genera *Stictis* and *Nanostictis*.

### *Nanostictis* gen. nov.

*Apothecia patelliformia, sessilia, albohyalina, minima, erumpentia, excipulo pseudo-parenchymatico praedita. Margo excipuli bene evoluta, crenulata. Pars parietis excipuli hymenio adhaerens et in idem sensim transiens. Asci cylindrico-clavati, apice rotundato et ibi cum membrana valde incrassata, poro apicali dehiscentes, 6–8 sporas continentes. Ascosporae hyalinae, filiformes, parummodo contortae, parallelae, indistincte septatae. Paraphyses rectae, hyalinae, filiformes, indistincte septatae, supra claviformiter vel irregulariter incrassatae, ascos non superantes.*

*Typus:*

### *Nanostictis peltigerae* sp. nov.

*Apothecia patelliformia, sessilia, albohyalina, minima (0.16–0.32 mm. diam.), erumpentia, sparsa vel plus minusve gregaria. Margo excipuli bene evoluta, e typo "textura globulosa" vel "textura angularis", crenulata. Asci cylindrico-clavati, 50–64  $\mu$  alti, 4.0–4.8  $\mu$  lati, 6–8 sporas continentes, membrana apicalis 2.5–4  $\mu$  crassa, iodo non mutatur. Ascosporae hyalinae, filiformes, parummodo contortae, parallelae, 40–60  $\mu$  longae, 0.8–1.3  $\mu$  latae, indistincte 3–4-septatae. Paraphyses rectae, filiformes, indistincte 3–5-septatae, supra claviformiter, rarius irregulariter incrassatae, vel interdum lanceolatae, ascos non superantes.*

*Hab.: Dania, in insula Anholt, in thallo emortuo Peltigerae polydactylae in Calluneto muscoso. Typus in Herbario Musei Botanici Hauniensis (legit autor mense Julio anno 1940, no. 5400).*



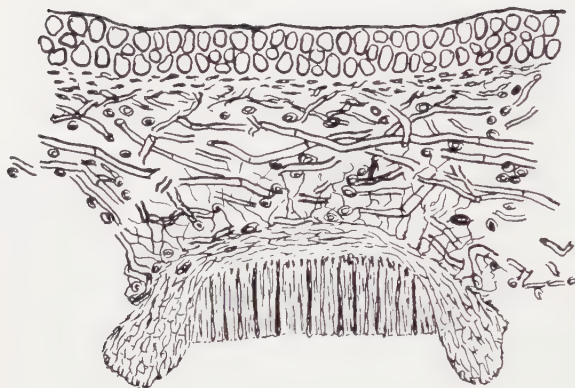


Fig. 1. Vertical section of *Peltigera* thallus with fully developed apothecium of *Nanostictis peltigerae* on the underside of the lichen thallus (170  $\times$ ).

The very minute, translucent white apothecia vary from 0.16–0.32 mm. in diam. and occur gregariously or more or less scattered on decaying parts of *Peltigera polydactyla* thallus, which have been shaded and killed by younger thallus-lobes of the same lichen. The degree of decay of the parts of lichen thallus infested with *Nanostictis peltigerae* is illustrated by the fact, that the algae with surrounding hyphae are shrivelled. Only the cortical layer and the medullary layer have retained their structure, being composed of more thick-walled hyphae. Remnants of protoplasm can be detected in these hyphae by coloration with lactophenol + cotton-blue. The very delicate hyphae (diameter 0.6–0.8  $\mu$  including membrane) of *Nanostictis* are seen growing between the coarse *Peltigera* hyphae (see Figs. 1–3). *Nanostictis peltigerae* is evidently saprophytic.

In its initial stages the apothecium is globose and enclosed between the hyphae of the lichen, later the apothecia are breaking through to the surface. The apothecia of *Nanostictis* appear mostly on the underside of the *Peltigera* thallus, as no cortical layer is developed here. Occasionally some apothecia are found on the upper surface, but only where the cortex of the lichen is more decomposed (see Figs. 1 and 2).

The mature apothecia are dish-shaped with a prominent margin of the excipulum. This margin is crenulate and dull white when dry, because the globular cells in its upper parts are devoid of protoplasm and filled with air. When moistened the apothecia get almost invisible. The apothecia of *Stictis* have a very strong habitual likeness to those of *Nanostictis*. The same velvety whiteness of the crenulate or lobate margin of the excipulum characterizes the apothecia breaking through the surface of the substratum. The structure of the excipulum is, however, quite different in the two genera.

Fig. 2. Vertical section of *Peltigera* thallus with a young, just opened apothecium of *Nanostictis peltigerae* breaking through the cortex on the upper surface of the lichen. The cortical layer of the lichen is more decomposed in this part of the lichen thallus than in the section pictured in fig. 1 (170  $\times$ ).



#### Anatomy of the apothecium of *Nanostictis peltigerae* (see Fig. 3):

Excipulum (parietal part) composed of short celled, colourless hyphae, so firmly conglutinate, that it is impossible to distinguish the walls of the individual hyphae in sections ("textura globulosa" or "textura angularis", cfr. STARBÄCK, 1895, and KORF, 1951). Margin 50–60  $\mu$  thick, lumen of cells 1–5  $\mu$ . The part enclosing the hymenium is united with this layer, and a gradual transition is observable between the paraphyses and the innermost cell-rows of the excipulum. The bottom of the excipulum consists of very narrow hyphae, closely interwoven and conglutinate, lumen of the cells 0.5  $\times$  2.5–7  $\mu$ . From the outside of the excipulum very narrow hyphae issue, which spread in the lichen thallus. Parts of the substratum (i. e. *Peltigera* hyphae) are found enclosed in the tissue of the excipulum.

The hymenium is colourless, its elements are glued together by a gelatinous substance. Asci cylindrically club-shaped, 50–64  $\mu \times$  4.0–4.8  $\mu$ , with rounded, very thick-walled apex (2.5–4  $\mu$  thick), otherwise the ascus membrane is very thin. The spores are discharged through a pore in the top of the ascus, but this pore is very difficult to see before the ejaculation of the spores. (In *Stictis radiata* the thickening of the apical membrane is pierced through almost to the top by a very distinct pore.)

Spores hyaline, threadlike, 40–60  $\mu \times$  0.8–1.3  $\mu$ , 6–8 in ascus, somewhat twisted together in a bundle. The discharged spores are still twisted and cannot be seen lying in one plane in the preparations. The spores are indistinctly 3–4-septate, sometimes unseptate, one end is more attenuated than the other.

Paraphyses filiform, unbranched and indistinctly septate, 45–60  $\mu \times$  0.5–0.7  $\mu$ . The end cell is a little broader (to 2  $\mu$  thick), club shaped or lanceolate or more seldom irregularly thickened. The ends of the para-



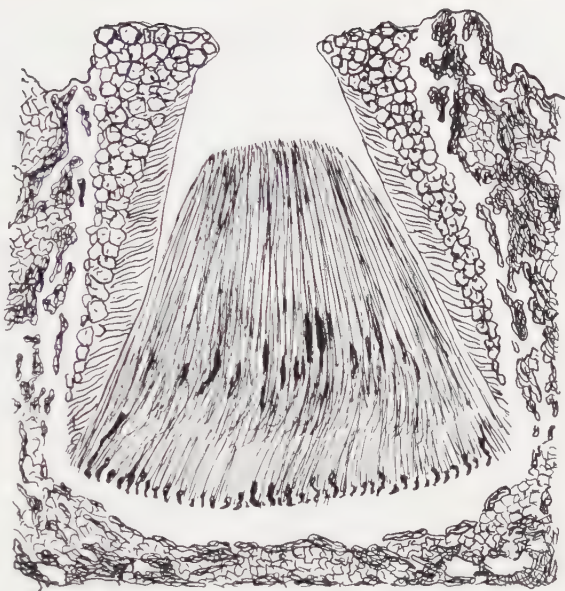
Fig. 3. *Nanostictis peltigerae*; a: asci, one ascus is twisted a little in the crush mount; b: spore; c: paraphysis and young ascus; d: different forms of paraphysis-tips (a–d are drawn from a crush mount coloured with lactophenol + acid fuchsin, according to MANEVAL, 1936); e: cross sections of two asci, drawn from a horizontal section through an apothecium; f: vertical section of marginal part of apothecium (1000  $\times$ ).

physes form no epithecium, and the asci rise above the paraphyses at maturity.

There is no positive reaction to iodine of asci and paraphyses.

The subhymenium consists of colourless hyphae, not easily distinguished from those of the bottom of the excipulum. Asci arise in fascicles from croziers.

Fig. 4. Vertical section of a young apothecium of *Stictis radiata* (L.) PERS. embedded in its substratum: secondary phloem of a decaying twig of *Salix* sp. The specimen pictured is collected in Boserup wood near Roskilde, Denmark, 2.10.1887, leg. O. ROSTRUP (190  $\times$ ).



*Nanostictis peltigerae* is only known from the type locality, where it was found growing on decaying parts of the thallus of *Peltigera polydactyla* on the ground in a mossy heath on a slope exposed to the north on the hill Nordbjærg (alt. 30 m. s. m.) on the island Anholt in Denmark. 24.7.1940, leg. M. SKYTTE CHRISTIANSEN, coll. no. 5400. Type specimen in the Botanical Museum of the University of Copenhagen.

In order to throw light on the relation of the new genus *Nanostictis* to the genus *Stictis* PERS. the autor has examined the structure of the apothecium of the type species of this genus: *Stictis radiata* (L.) PERS.

The apothecia of *Stictis radiata* are embedded in the substratum, and only the white margin of the excipulum is seen. At first the apothecia are closed at the top, then an aperture is formed through the growth of hymenium and excipulum (Fig. 4 shows a section through a young apothecium, the hymenium of which has been exposed a short time before the specimen was collected). In older apothecia the hymenium is broader and more exposed, and the excipulum grows upwards with a radiately lobed margin above the substratum (cfr. Fig. 3 on t. I in NANNFELDT's thesis (1932), which shows an old apothecium of *Stictis pupula* FR.).

In *Stictis radiata* the parietal part of the excipulum is separated from the hymenium down to the bottom of the excipulum. The inner side of the excipulum wall is covered with inwards pointing tips of hyphae,



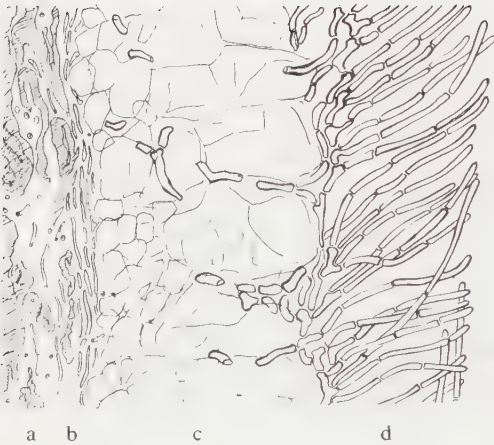


Fig. 5. Part of the same section as pictured in Fig. 4, showing structure of middle part of excipulum wall; a: secondary phloem of *Salix* sp., somewhat disintegrated, with mycelium of *Stictis radiata*; b: narrow, hyaline hyphae covering the outside of the excipulum; c: crystals of calcium oxalate with very few hyphae; d: inside of excipulum covered by projecting hyphae with free tips (1000  $\times$ ).

reminding of the periphyses of the pyrenomycetes (see Figs. 4 and 5). The excipulum wall is filled with crystals of calcium oxalate, only few hyphae are seen between the crystals. The outside of the excipulum wall is composed of narrow hyphae, forming transition to the mycelium in the substratum. The subhymenium and the bottom of the excipulum consists of colourless, thin-walled hyphae.

The genus *Stictis* as limited by NANNFELDT (1932) and REHM (1888, 1912) still contains heterogeneous elements. *Stictis fimbriata* SCHWEIN. must be excluded from this genus, i. a. on account of its different ascus structure (see PETRAK, 1947, p. 91). *S. cladoniae* (REHM) REHM must be excluded too on account of the structure of its excipulum ("Gehäuse parenchymatisch, dick, braun, glatt", REHM, 1882, p. 116, 1912, p. 159). Unfortunately I have seen no specimen of this species.

*S. elevata* KARSTEN is completely in accordance with the type species in the structure of the excipulum, and it might belong to the same species. *S. arundinacea* PERS. and *S. pupula* FR. agree well with the type species in the structure of the excipulum, which differs only in having dark and more thick-walled hyphae.

The systematic position of *Nanostictis*:

The genus *Nanostictis* must be placed in the order *Ostropales*, as it has the narrow ascus with thickened apex and filiform, parallel spores characteristic of this order (see NANNFELDT, 1932, p. 75). Within this order a great diversity is found regarding the form and structure of the apothecium. The following synopsis of the genera of *Ostropales* (modified after NANNFELDT, l. c., p. 77) will show the differences between *Nanostictis* and the already described genera of this order:



- A. Apothecia stalked, with convex hymenium . . . . . *Vibrissea*
- B. Apothecia unstalked, with plane hymenium.
  - I. Parietal part of the excipulum separated from the hymenium. Paraphyses unbranched, forming no epithecium with their tips . . . *Stictis*
  - II. Parietal part of excipulum united with the hymenium. A gradual transition is seen between the paraphyses and the innermost cell-rows of the excipulum.
    - 1. Parietal part of the excipulum consisting of thick-walled, brown hyphae ("textura intricata" or "textura oblita"). The branched ends of the paraphyses form an epithecium . . . . . *Schizoxylon*
    - 2. Parietal part of the excipulum of pseudoparenchymatic structure ("textura globulosa" or "textura prismatica"). The branched end of the paraphyses form an epithecium . . . . . *Apostemidium*
    - 3. Parietal part of the excipulum of pseudoparenchymatic structure. Paraphyses unbranched, not longer than the asci . . . . . *Nanostictis*
- C. Fruit-bodies resembling perithecia, immersed in the substratum . . . . .  
 . . . . . *Ostropa, Robergea*

The ascus typical of the order *Ostropales* is narrow cylindrical. In *Nanostictis* it is broader than usual, cylindrically club-shaped. INGOLD has however (1954, p. 13) described a species of the genus *Apostemidium*, *A. sporogyrum*, which has exactly the same form of the ascus.

### References.

- INGOLD, C. T., 1954: Aquatic Ascomycetes: Discomycetes from Lakes. Trans. Brit. Mycol. Soc. 37: 1-18.
- KORF, R. P., 1951: A Monograph of the Arachnopezizeae. Lloydia 14: 129-180.
- MANEVAL, W. E., 1936: Lactophenol Preparations. Stain Technology 11: 9-11.
- NANNFELDT, J. A., 1932: Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten. Nova Acta Reg. Soc. Sci. Upsalensis IV, 8, 2: 1-368, pl. 1-20.
- PETRAK, F., 1947: Über die Gattungen Naemacyclus Fuck. und Lasiostictis Sacc. Sydowia 1: 89-93.
- REHM, H., 1882: Beiträge zur Ascomyceten-Flora der deutschen Alpen und Vor-alpen. Hedwigia 21: 97-103, 113-123.
- 1888: Ascomyceten: Hysteriaceen und Discomyceten, pp. 65-208. Dr. L. RABENHORST's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. 2. Aufl. I. III. Abth., VI + 1275 pp., 1887-1896.
- 1912: Zur Kenntnis der Discomyceten Deutschlands, Deutsch-Österreichs und der Schweiz. Ber. Bayer. Bot. Ges. 13, 102-206.
- STARBÄCK, K., 1895: Discomyceten-Studien. Bihang t. K. Svenska Vet.-Akad. Handl. 21, III, 5: 1-42, tab. 1.

## Iagttagelser over *Smyrnum perfoliatum* L.

Af ERNST FLOTO

*Smyrnum perfoliatum* L., Lundgylden, der horer hjemme i Middelhavslandene og Kaukasus, angives i botaniske værker oftest at være en to-årig urt. At dette ikke kan være tilfældet vil fremgå af de nedenfor nævnte iagttagelser, der er gjort indenfor Universitetets botaniske Have.

*Smyrnum perfoliatum* er ikke meget kendt her i landet, den anvendes dog undertiden som prydpilante under større træer i åben, skovagtig bevoksning. Som prydpilante har den en vis værdi, navnlig fordi den tåler halvskygge og kan danne en tæt bundvegetation, der i blomstringstiden om foråret udmærker sig ved sin iøjnefaldende gyldengule farve. Den er da også fundet værdig til omtale både i Nordisk illustreret Havebrugsleksikon og i Berlingske Have-Leksikon. I afskåret tilstand holder planten længe i vand, og den kan derfor anvendes til dekoration i større vaser.

Slægten *Smyrnum*, som horer til *Umbelliferae*, omfatter ialt syv arter og udgør ifølge WARMING: Frøplanterne, sammen med *Conium* en særlig gruppe, *Smyrnum*-gruppen, indenfor *Apium*-underfamilien. Delfrugterne hos denne gruppe er furede, glatte og stærkt hvælvede. På bugsiden hænger de to spaltefrugter sammen i en stribe eller smal flade. Ved modningen er frugterne sorte.

Tre af *Smyrnum*-slægtens arter findes i Sydeuropa; de to af disse har langt tilbage i tiden været dyrket i de botaniske haver i København, nemlig *S. olusatrum* og *S. perfoliatum*. *S. olusatrum* L., der tidligere har fundet anvendelse som krydderurt, kan i Botanisk Haves journaler følges tilbage til år 1802 og *S. perfoliatum*, der har medicinsk anvendelse, forekommer i havens bøger så langt tilbage som i året 1795. Sidstnævnte har dog ikke siden nævnte år og indtil 1931 været dyrket kontinuerligt i haven, gentagne gange har man i dette tidsrum måttet rekvirere frø fra fremmede botaniske haver. Dette forhold skyldes ikke, at planten er vanskelig at dyrke her i landet, hvor de klimatiske forhold tværtimod

passer den særdeles godt. Dens fraværelse i perioder står derimod i nøje forbindelse med plantens livslob, hvilket man i tidligere tid sandsynligvis ikke har haft tilstrækkeligt kendskab til. Den passer ikke til den dyrkningsmåde, man anvender for stauder og to-årige urter.

Ifølge HEGI: Flora von Mittel-Europa, vokser *S. perfoliatum* imellem græs i buskagtige bevoksninger og i lyse skove nær kysterne. Samme sted anføres, at planten ofte dyrkes i haver, især i botaniske, hvori og i hvis nærmeste omgivelser den ofte forvilder sig. I slotshaven ved Schweitzingen i Baden skal planten således have vokset vild i over 50 år, og den: „verhält sich hier als einjährige Pflanze, die sich jedes Jahr selbst aussät.“

At planten som citeret skulle kunne være en-årig er ganske udelukket, som nævnt angives den at være to-årig, hvilket også – bortset fra ovennævnte citat – er tilfældet i Flora von Mittel-Europa og i COSTE: Flore de la France. Efter de iagttagelser der er gjort, kan *S. perfoliatum* aldeles ikke, selv under de mest gunstige forhold, gennemføre sit livslob hverken på eet eller på to år.

*Smyrnium perfoliatum* er en enstænglet, indtil meterhøj knoldvækst med forgrenet blomsterstand. Grundbladene er een til flere gange 3-delt-snitdelte, glatte og stilkede, de øvre stængelblade er siddende og udelte med hjerteformet grund; lapperne rager over hinanden, hvorved det ser ud som om bladet var gennemvokset, hvilket det latinske artsnavn, der altså er misvisende, hentyder til. Den øverste del af stængelen er vinget. Som nævnt er højbladenes farve under blomstringen smukt gyldengul, hvilket især fremhæves, når planten vokser under træer og solens stråler rammer den gennem de endnu bladløse trækroner – heraf det meget betegnende danske navn Lundgylde.

I et af de nævnte havebrugs-leksika er anført, at frøet skal sås i maj måned, hvilket imidlertid ikke er noget formålstjentligt tidspunkt, idet frøet i så fald først spirer i det følgende forår. Som den skyggetålende plante *S. perfoliatum* er, må den på det tidspunkt, hvor træerne er ved at udvikle blade, d.v.s. omkring midten af maj måned, have nået sin maksimale udvikling indenfor pågældende vækstsæson. Spiring og vækst viser sig da også at være knyttet til ganske bestemte årstider. Når de træer, hvorunder *Smyrnium* normalt vokser, har fuldt udviklede blade og derved giver tæt skygge samtidig med, at vandforbruget hos dem er stort, går *Smyrnium* til hvile, men som tilfældet er med andre frilands-knoldvækster, vil væksten igen begynde med indtrædende efterårsfugtighed. Sidst i november måned vil man således finde, at planterne under jorden allerede er ved at udvikle blade, og i milde vintre kan friske blade allerede ses i januar måned samtidig med at *Eranthis* begynder at vise sig.



Fig. 1. Frøplante af *Smyrnium olusatrum*. Kimbladstilkenes nedre del er vokset sammen til et rør i hvis bund kimknoppen befinder sig.



Fig. 2. Kimplante af *Smyrnium perfoliatum*. Det stængellignende organ mellem kimbladene og knolden er dannet af de sammenvoksede kimbladstilke.

Med det formål for øje at muliggøre mere indgående iagttagelser over plantens varighed, livsform m. m. blev der i sommeren 1946 straks efter frøets modning udsået en 20 m lang række frø på et areal, hvor der i forvejen ikke fandtes planter af *Smyrnium*. Dette frø spirede i foråret 1947, og det frembragte en bestand på ca. 500 planter.

I flere henseender er der stor forskel på de to nævnte *Smyrnium*-arter. På fig. 1 ses en frøplante af *Smyrnium olusatrum*. Hos denne art er kimbladstilkenes nedre del vokset sammen til et synligt rør; i bunden af dette,

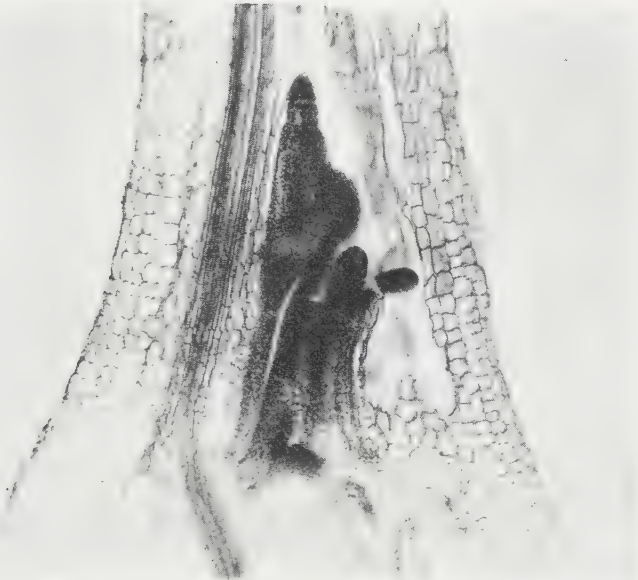


Fig. 3. Snit gennem den øverste del af en ganske ung knold af *Smyrnium perfoliatum* visende kimknoppen, der er den eneste knop denne art danner i sine fire (eller tre) leveår.

ca. 1 cm under jordoverfladen, findes kimknoppen. Frøet af *S. olusatrum* spirer i det tidlige forår, udvikler samme år løvblade og danner en grenet rodknold, hvorfra der året efter fremkommer blomsterstængel.

I modsætning til *S. olusatrum* udvikler *S. perfoliatum* i første leveår kun kimblade, og kimbladstilkene er hos denne i hele deres længde vokset sammen til et kompakt hypocotyllignende organ, som fortsætter ned i jorden til 8–10 cm's dybde. Den nedre del af dette organ er næsten hårfint, og kun i sandet jord er det ved omhyggelig opgravning muligt at få kimplanterne ubeskadiget op af jorden. Til præparation blev derfor anvendt planter, der var dyrket i vand.

I fuldt udviklet tilstand er kimbladene 3–4 cm lange, af form er de aflangt ovale og tilspidsede mod basis. Over jorden er det hypocotyllignende organ ca. 5 cm langt, kimknoppen vil derfor befinde sig 13–15 cm under kimbladpladerne. I plantens første leveår opfører den sig analogt med *Anemone apennina*, *Bunium bulbocastanum*, nogle *Corydalis*-arter og *Eranthis*, der i naturen vokser under tilsvarende kår, d.v.s. under træer eller buske, men i modsætning til de nævnte planter, der alle er perennerende, er *S. perfoliatum* en udpræget hapaxant.

I løbet af første sommer, hvor som nævnt kun kimbladene udvikles,



danner *S. perfoliatum* en indtil ærtestor roeformet knold, som vistnok må betragtes som værende en ren hypocotylknold, se fig. 2.

Fra knolden fremkommer i plantens andet leveår et eller to løvblade, som dog kun under meget gode vilkår er i stand til at assimilere tilstrækkeligt til, at planten i sit tredje leveår kan bringes til blomstring. Af de ca. 500 forsøgsplanter udviklede kun 10 blomsterstængler i året 1949, d.v.s. ca. 2%. Så godt som alle resterende forsøgsplanter blomstrede i året 1950, d.v.s. i deres fjerde leveår. En veludviklet knold er 4–5 cm lang, men en del knolde var på blomstringsstadiet betydelig mindre, det synes derfor ikke alene at være knoldens størrelse som betinger blomsterstænglernes udvikling.

Efter blomstring og frugtsætning dør planterne; det samme er tilfældet, når blomsterstænglen afskæres over grundbladene så snart den viser sig. Med andre ord er planten i sine fire (eller tre) leveår ikke i stand til at udvikle andre knopper end kimknoppen.

Undersøgelsen viser tydeligt, at *Smyrnum perfoliatum* er en fler-årig, een gang blomstrende knoldvækst – eller en pleiocyklisk hapaxant.

Såvel i Universitetets botaniske Have som i haven ved Den kongelige Veterinær- og Landbohøjskole viser Lundgylden sig at være i besiddelse af stor vitalitet og formeringsevne. Hvor den vokser i mængde fortrænger den alle mindre planter. I førstnævnte have har den forvildet sig overalt.

## Summary.

### Observations on *Smyrnum perfoliatum*.

In botanical works *Smyrnum perfoliatum* is stated as being a biennial. Investigations concerning the cyclus of the plant were made in the Botanical Garden of the University of Copenhagen in the years 1946–50. It was observed that the plant as a rule uses four seasons of growth to reach the flowering stage (only two per cent of c. 500 plants developed flowers in their third year). Seeds sown immediately after ripening will not germinate till next spring and only the cotyledons will appear first year. The stalks of the cotyledons are connated in a hypocotyllike organ. The first year a little corm is developed 8–10 cm. below the soil surface. The cotyledon-bud appears on the top of the corm, (see Fig. 2). The plant dies after the ripening of the fruit in the fourth (or third) year. The same occurs if the flowerstem is removed immediately after its appearance, as the plant is unable to produce other buds than the cotyledonbud.

## The *Rhizocarpon* Species with Peltate Areoles Occurring in Europe and North America

By PAUL GELTING

After a sledging through the valley, which connects the Steenstrup lakes in the heart of the Nugssuaq peninsula, W. Greenland, with the trading post Sarqaq, I spent the light time of the day on October 30. 1949 in examining the lichens on a south exposed seepage in the gneiss area 2 km W. of the church in Sarqaq.

It was a rock with the common plants of seepages on gneiss in W. Greenland: *Ephebe lanata*, *Phylliscum Demangeonii*, *Physcia sciastra*, *Rhizocarpon geminatum* a. o., spread among an almost continuous crust of *Cyanophyceae* and dark, sterile Gloeolichens. Isolated tufts of *Andreaea rupestris* were incrustated by *Crocynia neglecta*, *Massalongia carnosae* and *Polychidium muscicola*. From the steep rock, partially ice covered, a large icicle was pointing towards the clear ice of a frozen rock-pool. *Lecidea Dicksonii* and grey green specimens of the *gibbosa* group of *Lecanora* were common here. Suddenly I observed through the ice of the steep rock a lichen, which I had never noticed before. Seemingly red brown apothecia on a black hypothallus. By aid of hammer and chisel I succeeded in collecting it. As the weather was growing cold and the light failing, I went towards the trading post just as the land wind was coming up.

The find was actualized again, when in 1950 I found the species in Lyngmarken at Godhavn on Disko Island. An examination in the laboratory of the Arctic Station, my home for eight years, showed that, what in the field I had taken for apothecia, were areoles. Fortunately the Lyngmark specimens had true apothecia too, but turned undeterminable after European keys. Later, on consulting FINK: Lich. flora of United States, the species was determined as *Rhizocarpon Bolanderi*, a species then not known outside the Pacific States of U.S.A. Travelling along the Greenland coast in 1951, I found the species at many localities, and

having found it only on gneiss, I sought in the years 1951–1953 intensively for it on basalt, but without success. Instead I found here another peltate areoled, brown *Rhizocarpon*, in the following described as *Rhizocarpon arctogenum* n. sp.

A third species with peltate areoles, *Rh. rittokense*, is common on gneiss in W. Greenland, and a fourth, *Rh. leptolepis*, also on silicious rocks, is not known outside Europe. Besides these no other peltate *Rhizocarpon* is known to me. *Rh. arcticum* Räs., described as “subsimilis *Rh. leptolepi*”, does not belong here; it is a taxonomically insignificant modification of *Rh. grande*, infested by *Tichothecium pygmaeum* as shown by the type in Helsingfors.

The working up of the material for this publication has partly been done at the Danish Arctic Station in Godhavn, W. Greenland, partly at the Institute of Systematic Botany of the University of Uppsala. To Professor J. A. NANNFELDT and his staff, especially Docent ROLF SANTESSON, I express my cordial thanks. Through the courtesy of Professor G. E. DU RIETZ the microphotographs could be produced at the Institute of Plant Geography in Uppsala. Miss MARGARET NORRISH has kindly corrected my English. For loan of herbarium material I am indebted to Docent GUNNAR DEGELIUS, Professor G. E. DU RIETZ, Fil. Dr. A. H. MAGNUSSON and to the botanical institutes of Åbo, Copenhagen, Helsingfors, München, Oslo, Stockholm, and Uppsala. Abbreviations of herbaria as in LANJOUW and STAFLEU: Index Herbariorum I, 1952. Numbers cited in paranthesis are field or herbarium numbers.

Until adequate terms for the different structural parts of the apothecium have been proposed (cf. Internat. Bot. Congr. Stockholm 1950. Proceedings 1954, 812) those commonly used for *Rhizocarpon* may be useful.

Excipulum is in our group a typical excipulum proprium in the sense of FRIES (1831, p. LXIV); the details of its structure as given below, however, refer mainly to its lateral part. Unfortunately in lichenological literature the concept of hypothecium is not clear and includes different structural elements. Inside excipulum we find in *Rhizocarpon* a brown tissue, which KÖRBER (1855), TH. FRIES (1874), VAINIO (1922) and later writers place with the hypothecium. In young apothecia this tissue often forms a rather thin and flat cupula, in older ones it attains considerable dimensions, forming a lenticular or almost semiglobular pulpa, filling the space between excipulum and the paraphysogenous tissue. Against its placing with excipulum speaks the fact, that it rests upon a characteristic and complete excipulum, against its classing with hypothecium the fact, that it is superposed by the paraphysogenous tissue. It is a structural unit (to almost the same degree as is the thalline medulla), which I in want of a better designation, call pulpa.

In keeping pulpa distinct from the paraphysogenous tissue (cf. p. 79) and from the ascogenous cells, I have tried to contribute to a more exact interpretation

and to make a distinction possibly fit for further use. It seems clear to me, that the concept of hypothecium would gain in value and make ideas clearer, if it could be confined to one single tissue and not, as hitherto, be applied to a complex of different tissues. In order to avoid confusion I have not in this paper used the term hypothecium.

Besides keeping pulpa distinct, I have also tried, at least theoretically to keep the paraphysogenous tissue apart from the ascogenous, being well aware, that the distinction between the two categories of cells may be difficult in practice as long as a differentiating staining is not easily produced and as long as our knowledge as to the uniplot and the diplont, thus the caryology of the ascogenous cells, is still insufficient.

The hymenium is measured from base to top of paraphyses. By epithecium is meant the upper, coloured part of hymenium. Description of asci and spores has conventionally been placed after the description of hymenium, this causing no confusion. It would, however, be happy if future terminology could consider the possibility of keeping the diploid phase (asci) and the ascogenous cells apart from the haploid (e. g. pulpa, paraphysogenous tissue, paraphyses).

Besides in *Rhizocarpon*, a well developed and conspicuous pulpa is found in many other genera with lecideoid apothecia e. g. *Bacidia*, *Buellia*, *Lecidea*. It may, however, also be well developed in genera with lecanoroid apothecia, in the genus *Lecanora* often uncoloured (cf. GALLØE: I-IX, 1927-54, where beautifully illustrated and variously named). In the Discomycetes it may be conspicuous too, as appears from several of the microphotographs in NANNFELDT (1932).

All observations and measurements given below are made by the writer. Measurements of inner structural elements are taken in water or lactic blue. Sections made for preliminary orientation in Greenland are hand cuts after the handy method of MAGNUSSON; those for final description are freezing microtome sections 5-10-15  $\mu$  thick. Staining agencies: Lactic blue, phloxine and erythrosine.

### General Appearance.

Peculiar to the four species is the outer appearance, characterized by the well defined, brown, peltate and marginated areoles, constricted below, dispersed or grouped, sometimes touching, on a black, conspicuous hypothallus. Areoles round or polygonal, rarely variously lobed or incised; upper surface concave, subplane or convex, shining or matt, at times pruinose near margin. Areolar margin mostly prominent (10-100  $\mu$  high, 60-120  $\mu$  broad), black or greyish pulverulent (when old and decorticated white), rarely subcrenulate, at times disappearing. Lower surface dark, matt, narrowly attached to hypothallus.

From the squamulose areole the peltate areole differs in being marginate, almost recalling an eulecanoroid apothecium. In hardly any group or

species within the genus is the individuality of the particular areoles so distinct: They are well constricted below, surrounded by a margin and do not divide into minor areoles. It seems as if they were in life and death independent.

Apothecia small and inconspicuous in spite of their being generally larger than the surrounding areoles, dispersed or grouped 3–7 together, adnate or sessile on the hypothallus; disc black, when old rugulose, plane or convex; margin thick or thin, black, subpersistent or disappearing.

Seen at a distance the specimens look black; under a lens the brown areoles are conspicuous; apothecia first seen, when sought for, being dark and merge with the hypothallus.

### Structure of Thallus and Apothecia.

Hypothallus black, diffuse or radiating, bordering the thallus, however, generally well visible between the areoles too, giving the specimen its black appearance. Thickness varying from  $5\text{--}7\mu$  (one single cell layer) to  $20\text{--}30\mu$  or more. Cells globoid,  $4\text{--}7\mu$  in diam., or more or less stretched. Colour of hyphae black or greyish, with or without violet tinge. Uncoloured or decolorate cells often seen in upper part, possibly also present in the interior too. K—, or K+ slightly violet.

### Areoles.

Peltate; margin covered by lower cortex (cf. p. 77). In sections it is possible to distinguish (from above): Stratum decoloratum, upper cortex, algal layer, medulla, lower cortex.

The coloured parts of areole, as seen in sections under the microscope, are brown, or brownish violet (hardly purplish), often with a dark tinge. In thick sections, or in tissues, where colouring matter is abundant, the colour is dark or black. Medulla may partially be greyish, or matt, but generally uncoloured (macroscopically white). Green is seen in the chloroplasts of algae only. A yellowish or quite decolorate stratum forms the uppermost layer of the areole.

Decolorate stratum: Covering the upper surface within the margin(s). Colourless or slightly yellow brown, amorphous or in lower part with almost horizontal, slightly undulating striae (cf. GALLOE: III, 1930, 65–91 and Fig. 215). It is a kind of necral layer.

Upper cortex situated below decolorate stratum, extending laterally to inner edge of areolar margin. End cells swollen, globoid or pear



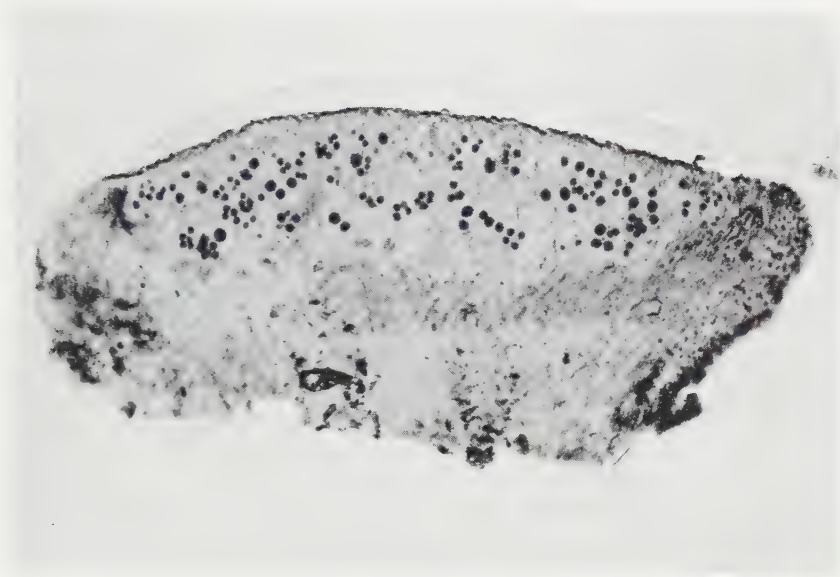


Fig. 1. *Rhizocarpon arctogenum* GELT. Section of areole (type),  $10\mu$  thick. Showing stratum decoloratum, upper cortical end cell layer, upper cortex, algal layer, medulla and lower cortex. Cf. the text. ( $\times 125$ ). SVEN ERIKSSON phot.

shaped, often flattened at top,  $4-6$  ( $8$ )  $\mu$  broad; brown colour often restricted to apical and lateral walls. Being the only part of upper cortex, which is more intensively coloured, the end cell layer is very distinct, the more so as the end cells are nearly in the same niveau, being rarely displaced more than their half length in relation to each other, young ones (with rather thin and rounded top) below, older ones (with flattened top) above the common niveau. The latter cells are near the end of their life, being finally pushed off by the younger ones, ending in the decolorate stratum, where their apical walls for some time may be noted as striae in the otherwise amorphous stratum.

Colourless part of upper cortical hyphae nearly vertical, forming almost a paraplectenchymatic cortex (as in GALLOE 1930, Fig. 215) with more or less isodiametric articuli,  $5-6\mu$  broad. Thickness of cortex small, being formed of few or rather few articuli,  $2-10$  in numbers.

Algal layer situated below upper cortex, extending laterally a little farther than this, penetrating under, rarely into, lower part of areolar margin. Occupying vertically from about one fourth to more than half of areolar height; in young areoles often almost filling the whole interior. Algae grouped in insular parties or equally dispersed. Hyphae  $4-6\mu$

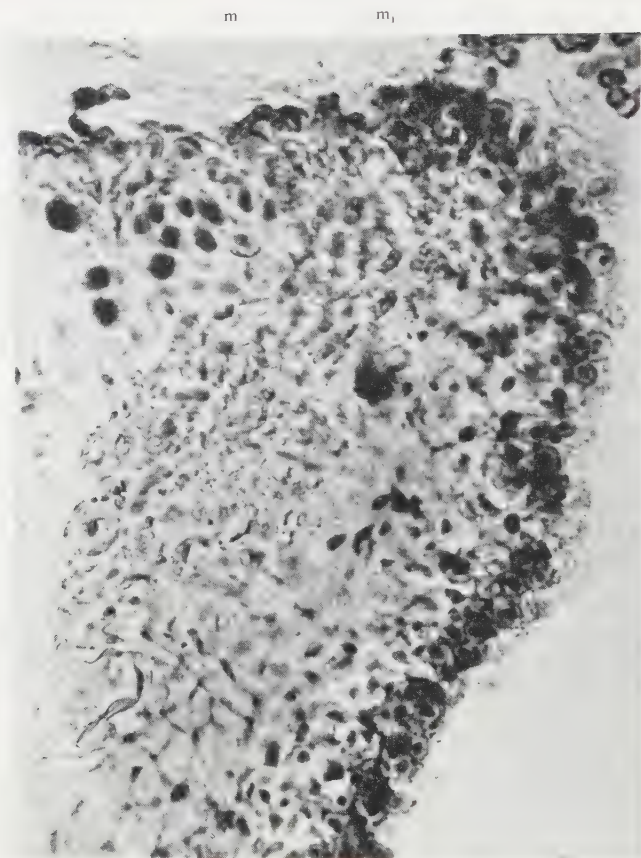


Fig. 2. Detail of Fig. 1, showing the areolar margin and the meeting point (m) of upper and lower cortex. To the left of meeting point the decolorate stratum, to the right clustered, decolorate end cells of lower cortex. At  $m_1$  a new meeting point is being established. Cf. the text. ( $\times 500$ )

SVEN ERIKSSON phot.

thick, with  $4-7\mu$  articuli, lumina  $2-3(4)\mu$  broad,  $4-6\mu$  long. Orientation of hyphae mainly vertical or radiate (diverging upwards and outwards); algal islets isolated from each other by vertical or radiating strands of hyphae, coming from medulla and going to upper cortex. Lower limit of algal layer more diffuse than upper; density of algae largest in upper or middle part.

Algae green, globoid, rarely ellipsoid,  $6-16\mu$  in diam., membrane  $1-1.2\mu$ ; after the form of the chloroplast they may belong to the genus *Cystococcus*.

Medulla uncoloured; occupying the space between algal layer and lower cortex; filling the interior of areole. Hyphae of thickness and articulation almost as in algal layer; orientation vertical, radiate or irregular; forming a loose, medullary tissue, which in sections of  $5-10\mu$  thickness shows the hyphal structure (almost as in GALLOE, 1930. Fig. 205, 214, 218). Through a dark tissue in the lower part, the areole is attached.

Lower cortex dark, covering the lower surface of areole. Outer part darker than inner. In thin sections the hyphae are seen running towards outer (and lower) surface of areole, ending with a  $5-8\mu$  broad, almost globular, pachydermatic cell, generally the darkest in the whole areolar section. End cell nearest articuli dark and pachydermatic too. End cells not flattened at top and forming not so particularly distinct a layer as that of upper cortex. The dark colour, however, is very impressive. A decolorate stratum absent; isolated or clustered, dead, decolorate end cells, still globoid, however, often adhering to lower cortex some time before falling off.

Areolar margin: The meeting point of upper and lower cortex (cf. Fig. 2) is generally situated, not at the top of areolar margin, but at its inner edge. The whole surface of margin thus covered by lower cortex. This holds good principally for alle four species and is beautifully seen in *Rh. Bolanderi* and *Rh. rittokense*. In *Rh. leptolepis* the meeting point may be variously displaced in accordance with the subcrenulate nature of its margin. In *Rh. arctogenum* the marginal cortex is covered by a stratum rather reminiscent of stratum decoloratum, however, differing in the cells being globoid (cf. Fig. 2). In all species medulla enters the margin, when typical and well developed.

Pruina: The pruina of upper surface originates from the decolorate stratum, this being variously broken up and loosening. The pruina of the areolar margin itself, however, are isolated or small clusters of dead end cells of lower cortex, giving the margin its subpulverulent appearance. (The white colour often seen, especially in old margins of *Rh. Bolanderi* and *Rh. rittokense*, is due to medulla, being visible when cortex has been removed in some way or other.)

Chemical reactions: The thalline reactions with K. C. J. and P. are rather varying. They are mostly of little taxonomical use in separating our species, but may perhaps prove of interest in search of special active or inactive minor taxa. They should be further studied.

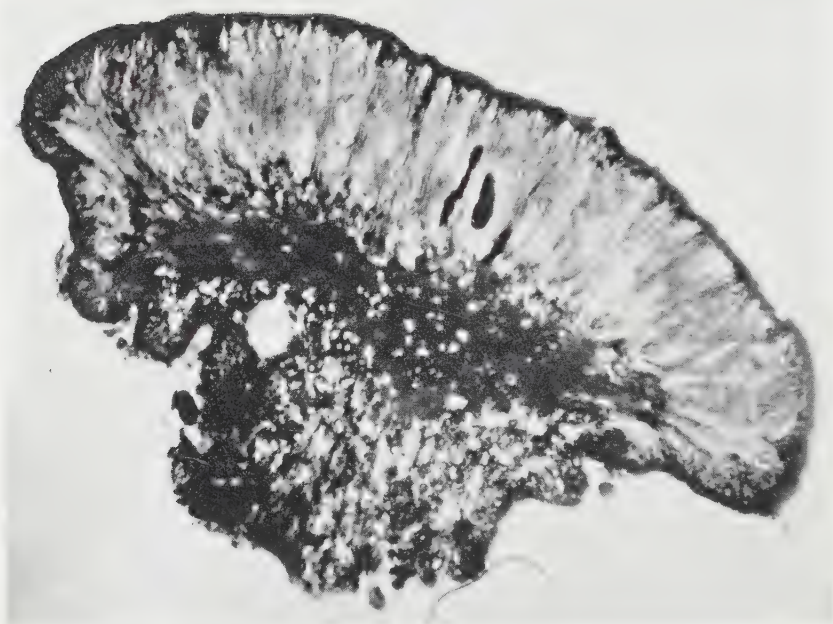


Fig. 3. Section of apothecium of *Rhizocarpon arctogenum* (type)  $10\mu$  thick. The dark pulpa downward limited by a greyish (lighter), hypothalloid tissue, forming almost a "stalk". The two lobes to the left are formed by lower part of excipulum. Being more than  $10\mu$  broad most spores has been carried out of the section by the cutting.

Staining: Phloxine. ( $\times 125$ ). SVEN ERIKSSON phot.

### Apothecia.

Lecideine; proper margin formed by upper part of excipulum. In sections it is possible to distinguish (from below): Excipulum, pulpa, paraphysogenous tissue, paraphyses; the three last mentioned imbedding the ascogenous tissue, asci and the spores. Coloured parts, as seen in microscope, generally brown or dark brownish (thick sections black), with or without violet tinge. Other colours not met with generally. Colouring matter bound to outer part of membranes.

Excipulum: Forming the outer envelope of the apothecium. Varying in thickness. Upper part  $10-80\mu$ , lateral part  $30-100\mu$ , basal part  $30-120\mu$  thick. Upper part dark, with vertically orientated, pachydermatic hyphae. Lateral and basal parts differentiated in two zones. The dark to black outer zone, almost paraplectenchymatic, hyphae constrictedly septate, cells pachydermatic,  $5-7\mu$  broad, isodiametric or slightly



stretched. The inner zone lighter coloured to uncoloured, cells more thinwalled, lumina larger. Orientation of hyphae in lateral part almost horizontal, in basal part vertical, running downwards.

Pulpa: Brown, darker than inner zone of excipulum; K—, J— occupying the space between excipulum and the paraphysogenous tissue (cf. below); varying in form from a thin, flat cupula to almost lenticular or semiglobular, and varying in thickness too, being quite thin or up to  $200\mu$  thick or more. Orientation of hyphae vertical or radiate; hyphal structure not easily seen on account of abundance of colouring matter; cells at times up to  $10\mu$  broad, generally very poor in protoplasm. Interstitial openings up to  $20\mu$  broad and still longer; tissue nevertheless firm. The limit of pulpa toward excipulum and the paraphysogenous tissue rather distinct. Centrally the basal part of pulpa is through a shorter or longer, dark tissue connected with hypothallus.

Having connection downwards with hypothallus the pulpa may possibly be presumed to have differentiated from this in an early stage of the apothecial primordium. In the fully differentiated apothecium pulpa has many functions. It is the imbedding (and transporting?) medium for the ascogenous cells; the supporting main element of the whole apothecium and as such a podium for the paraphysogenous cells and the hymenium. Its growth from a thin cupula to a thick lenticular or semiglobular pulpa is reflected in the outer shape of the apothecium and co-ordinate with the well known increasing convexity of the apothecial disc.

Hypothecium: (cf. p. 72–73).

Ascogenous cells and paraphysogenous tissue. Besides the brown pulpal hyphae we find below the hymenium two other categories of cells, both uncoloured and both taking a rather intensive blue colour in lactic blue. For the largest of these cells I have accepted the commonly used term: ascogenous cells; for the smallest, which form a continuous layer just below the hymenium, I have after some hesitation and provisionally accepted the name used by GALLOE (1929, p. 19): paraphysogenous tissue.

The ascogenous cells are situated above or more frequently imbedded in upper part of pulpa, isolated cells being immersed until  $60\mu$  or more. They form no continuous horizontal layer, on the contrary they are occasionally arranged in vertical or slightly radiating rows, ascending from the interior of pulpa towards its surface. They are rather large, globoid, up to  $15\mu$  in diam. On the surface of pulpa they rest isolated or more frequently clustered in small groups. There are little doubts that they are homologous with what in other genera is mentioned ascogenous



cells, in spite of the fact, that I never have had opportunity to observe the connection itself between these cells and the asci.

The paraphysogenous tissue is situated above or slightly imbedded in uppermost part of pulpa, in the latter case often more or less hidden by the brown colouring matter of the pulpal hyphae. It consists of small, isodiametric cells,  $3-4\mu$  in diam., lumina  $1-2\mu$  broad, forming a continuous, thicker or thinner layer between or near lower end of the paraphyses. So far as can be judged, it is from these cells (or very many of these cells) that the paraphyses originate, but here again the connection of the individual paraphyse with its mother cell is difficult to observe. An analogous tissue (very likely homologous too) in *Lecidea* is by VAINIO (1934, p. 168-179) called hypothecium subhymeniale.

In places ascogenous cells, easily recognised by their size, is imbedded as "nests with eggs" in the paraphysogenous tissue. Small ascogenous cells, however, of almost the same size as the paraphysogenous, will, if present, unfortunately not be distinguishable before differentiating staining agencies have been brought in use, or a caryological examination has been carried out in each separate case and for each separate cell, the paraphysogenous cells being haploid the ascogenous diploid or in the dicaryon stage (functionally diploid).

Hymenium uncoloured or with a faint violet tinge,  $100-150\mu$  high, J+ blue. Paraphyses rather loosely conglutinated (gelatine abundant), rather thin, slender, branched, septate below, constrictedly septate above. Upper articuli swollen, tips rather firmly conglutinated, top cell brown or brownish violet. Epithecium thus brown or brownish violet. Besides more or less dark brown paraphyses may occur too, giving in thick sections the hymenium a brownish colour. They should be further studied.

Asci saccate or inflated, 2-8 spored, lower end occasionally rather deeply ( $10-15\mu$ ) imbedded in pulpa.

Spores finally dark or darkened, variously septate, with distinct halo.

Chemical reactions: The reactions of coloured parts with K varying. Pulpa K—. Excipulum and epithecium K— or K+ more or less violet, occasionally with a faint, diffusing, brownish mist.

### Key to the species.

Areoles concave:

Spores 2, multilocular; thallus 3-7 cm.; areoles redbrown; areolar margin thick, prominent, incurved, sinuate; medulla J—.....  
 ..... *Rh. Bolanderi* (TUCK.) HERRE.

- Spores 8, uniseptate; thallus 3–10 cm.; areoles brown; areolar margin thinner, prominent, not sinuate; medulla J— (type), P—. . . . .  
 . . . . . *Rh. rittokense* (HELLB.) TH. FR.

Areoles convex:

- Spores 4, multilocular, oblong-ellipsoid; thallus 0.5–0.8 cm.; areoles brown; areolar margin thin, distinct; medulla J+ blue . . . . .  
 . . . . . *Rh. arctogenum* GELT.
- Spores 8, multilocular, broadly ellipsoid; thallus 2–6 cm.; areoles red brown; ar. margin indistinct, crenulate or disapp.; medulla J—. . . . .  
 . . . . . *Rh. leptolepis* ANZI.
- Spores 8, uniseptate; thallus 3–20 cm.; areolar margin rather thick; reactions with P varying . . . . . *Rh. rittokense* (HELLB.) TH. FR.  
 (aberrant types).

*Rhizocarpon arctogenum* GELT. n. sp.

*Thallus minutus, fuscus, areolis minutis, peltatis, marginatis, convexis vel subplanis, interdum nitidis, supra hypothallum nigrum dispersis vel aggregatis. Apothecia dispersa vel aggregata, inter areolis sita, sessilia vel adnata, minuta, disco atro, plano vel convexo, margine atro tenui cincto. Hymenium altum, superne fuscum vel fuscoviolaceum. Sporae 4 nae, multiloculatae, obscurae vel atrae, sat magnae.*

*Locus classicus: Insula Disko Groenlandiae, in rupe basaltica, Storstubben nominata, prope urbem Godhavn, 20 m. supra mare, legit PAUL GELTING (19967) 2.5.1953 (C).*

Icon: Fig. 1 p. 75. Fig. 2 p. 76. Fig. 3 p. 78. Fig. 4 p. 82.

Hypothallus black, edge diffuse or radiate, hyphae constrictedly septate, 4–7  $\mu$  broad, dark or greyish. K—. Thallus 0.5–0.8 cm in diam.; areoles slightly convex or subplane, round or polygonal, brown, often shining, pruinose towards margin. Margin thin, prominent or not, dark, more or less pulverulent. Lower side dark, rather broadly fixed to substratum. Thallus K—, KC—; medulla J+ blue, C— or C+ red, K—, KC—. Apothecia dispersed or grouped 3–7 together, adnate or sessile between the areoles, generally larger than surrounding areoles. Disc black, not pruinose, finally rugulose and slightly convex; margin black, thin, subpersistent or disappearing.

Areoles 0.4–0.8 mm in diam., 0.2–0.35 thick. Decolorate stratum 10–25  $\mu$  thick. Upper cortical end cells brown, 4–6 (7)  $\mu$  broad. Uncoloured cortex 10–20 (30)  $\mu$  thick, formed of 3–4 (6) articuli. Algal layer 45–80 (100)  $\mu$  deep, in thin areoles occupying up to half, in thick up to one third or one fourth of areolar height. Algae green, globoid, 6–12  $\mu$  in diam., membrane 1–1.2  $\mu$ , equally dispersed or grouped in islets. Medulla uncoloured, often greyish in upper part. Hyphae rather broad, 6–7 (8)  $\mu$ , towards base broader, 7–9  $\mu$ , constrictedly septate; articuli isodiametric

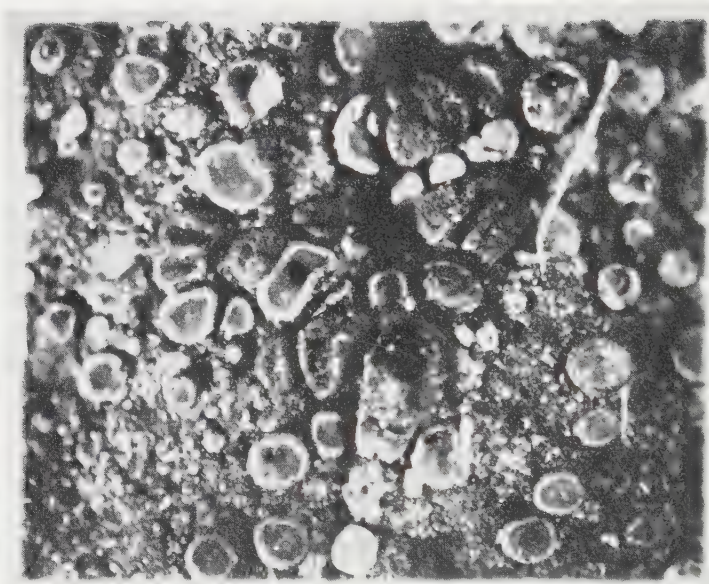


Fig. 4. *Rhizocarpon arctogenum* GELT. Habitus of specimen from same bit of stone as the type. ( $\times 15$ ). SVEN ERIKSSON phot.

or slightly stretched; hyphal structure well visible. Lower cortex brownish, cells varying in size,  $4-8\mu$  broad, nearly isodiametric, outermost 2-3 cells dark. End cells forming a rather uneven layer. Decolorate stratum absent on lower side, however, isolated or clustered, colourless, dead end cells, still globoid, often adhering.

Apothecia  $0.6-1$  mm in diam.,  $0.2-0.35$  mm thick. Excipulum  $40-60\mu$  thick in lateral part, thinner upwards, broader downwards, dark brown (often with slight violet tinge) in outer zone, lighter inwards. End cells nearly isodiametric,  $5-6$  ( $8$ )  $\mu$  broad; colouring matter bound to outer part of membrane. K— or slightly violet, without diffusing mist, or mist very faint. Pulpa up to  $500$  ( $700$ )  $\mu$  in diam., and up to  $220\mu$  thick; upper surface subconvex to convex; brown (thick sections black); orientation of hyphae vertical or radiate. K—, J—. Paraphysogenous tissue uncoloured, cells  $3-4\mu$  broad, lumina  $1-2\mu$ , forming a more or less distinct layer, up to  $25\mu$  thick, between or below lower end of paraphyses; at times seemingly imbedded in upper part of pulpa. Ascogenous cells uncoloured,  $8-10\mu$  broad, globoid, often deeply imbedded in pulpa and here forming vertical or radiating rows. Hymenium uncoloured or pale violet,  $120-150\mu$  high, J+ blue. Violet colour more distinct in K.

Paraphyses loosely conglutinated, often brown in lower part; branched, septate,  $2\mu$  broad in lower parts,  $3-4\mu$  at apices; uppermost articuli moderately swollen; top cell brown. Epithecium brown or slightly violet, K unaltered or more distinctly violet, without mist. Asci saccate or inflated,  $120-140 \times 30-40\mu$ . Spores 4 (5) in asci, multilocular, oblong ellipsoid  $31-42$  (50)  $\times$   $10-15$  (20) $\mu$ , often slightly bent. Young spores uncoloured, uniseptate, then for a time triseptate, uncoloured or smoky; finally dark and multilocular; loculi rather numerous; membrane  $1\mu$ ; halo  $1-2\mu$ , in K  $2-3\mu$ .

Characteristic for the new species are: the small size of thallus (smallest in the group), comprising rather few areoles, often only 10–15 in numbers, on a small, black hypothallus; the rather numerous apothecia (sterile specimens rarely met with), and their high relative density (3–7 apothecia pr. 10–15 areoles and per individuum is in this group a high density); the oblong, often slightly bent spores, being only 4–5 in asci. From *Rh. Bolanderi* it is easily kept apart by the small, convex areoles, the bent spores and their number. From *Rh. leptolepis* by the thicker areoles, smaller thallus size, and the form, colour and number of spores. From *Rh. rittokense* by the small size of thallus and areoles, septation of and number of spores. In one respect it differs from all the other species of the group, its incapacity of competition, an incapability most probably caused, at all events partially, by its small size.

Variation: Both in outer appearance (shape of areoles) as well as in inner structure (height of hymenium and size and form of spores) the variation is quite considerable. By sectioning numerous apothecia and areoles, from both same and different individuals, I have, however, found this variation characteristic of the species, and not, in the material at hand, a base for taxonomical division. The medullary reaction with C varies from specimen to specimen. The type individuum is C—, but in the same sample (same bit of stone) there are specimens reacting C— red.

Habitat ecology: All specimens seen from basalt; this being either solid rocks (dykes and breccia), blocks (up to 40 cm in diam.), boulders (up to 20 cm in diam.) or pebbles (2–4 cm in diam.). It prefers dry to slightly moist places near the ground. On rocks irrigated during snow-melting, it occurs at Godhavn with: *Caloplaca* cf. *lithophila*, *Crocynia arctica*, *Parmelia soresdiosa*, *Phylliscum Demangeonii*, *Rhizocarpon geminatum*, *Rh. geographicum*, *Rh. grande*. Very common on not or slightly coprically influenced blocks in *Vaccinium uliginosum*-*Dryas integrifolia* heaths with: *Candelariella vitellina*, *Lecidea micacea*, *L. stigmatea*, *Physcia ventosa*, *Sporastatia testudinea*, *Umbilicaria discolor*, *U. hyper-*



*borea*. In the wind-swept, almost naked gravel terraces at Røde Elv, herberging open societies of *Carex glacialis*, *C. rupestris*, *Papaver radicum*, *Poa glauca*, *Potentilla Vahlana*, *Saxifraga oppositifolia*, *S. tricuspidata* (all to *Dryadetum*), it is common on pebbles with: *Placynthium asperellum*, *Rhizocarpon geographicum*, *Rh. chionophilum*, *Rh. occidentale*. The species may thus be termed mesotrophous-eutrophous or mainly eutrophous. It is often snow free or but slightly snow-covered during winter. Prefers newly turned stones and young surfaces. It is a pioneer, ascending to considerable altitudes.

Distribution: Greenland. Hitherto only found on Disko Island, but probably to be found elsewhere in the Greenland basalt region.

Greenland. Disko Island. Godhavn: Storstubben (500 m. due E. of Arctic Station) 20 m. (19967, type); Stubbene, numerous places up to 60 m., thus at Guldklippen, (19931b); Elvebakken, pebbles on the ground (11610a-c); E. of Røde Elv, Elvesletten, pebbles at the foot ball ground (unnumbered); Brecciahøje, W. exp. seepage, 18 m. (20643d); Tunussua (= Tunorssuaq of the map), basalt block in wind swept, rich, morainic soil. 420 m., in front of glacier coming down from N. side of Skarvefjeld (19899a); all collected by GELTING.

### *Rhizocarpon Bolanderi* (TUCK.) HERRE

The lich. fl. Santa Cruz penins. California (Proceed. Washingt. Acad. Sci. XII, 2) 1910, 106. HASSE: Lich. fl. S. Californ. (Contr. Unit. States Nat. Herb. 17, 1) 1913, 57. ZAHLBRUCKNER: Catal. lich. univ. IV, 1927, 347. GRACE E. HOWARD: Lich. State of Washingt. 1950, 71. — *Buellia Bolanderi* TUCKERMAN: Gen. lich. 1872, 189, et: Synops. N. Am. lich. II, 1888, 103.

Type locality: Sandstone rocks in the Oakland hills, California, leg. H. N. BOLANDER (not seen).

Exs. CUMM. Lich. Bor. Am. Sec. ed. 75 (S). HASSE: Lich. ex. herb. HASSE. 247 (S).

Hypothallus black, rather thick; edge radiating or diffuse. Septa constricted, articuli dark. K—. Thallus 2–7 cm. in diam; areoles concave or subplane, brown or reddish brown, shining or matt; areolar margin thick, prominent, incurved, generally wavy sinuate, incised, black or grey, subpulverulent. Lower side of areole dark, often easily visible, narrowly fixed to substratum. Thallus K—, C—, KC—; medulla J—, K+ yellow, or K—, C—, KC—, P—.—Apothecia dispersed, adnate or sessile between the areoles. Disc black, not pruinose, finally rugulose and convex; margin black, subpersistent or disappearing.

Areoles 0.6–1.3 mm. in diam., 0.25–0.35 mm. thick. Decolorate stratum 20–40  $\mu$  thick, when old often falling off, leaving the white



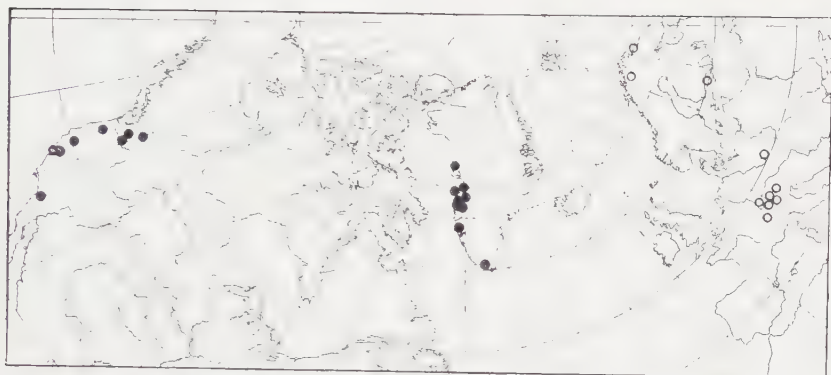


Fig. 5. Distribution of *Rhizocarpon Bolanderi* (black dots) and of *Rhizocarpon leptolepis* (open rings).

cortex exposed. Upper cortical end cells brown or brownish violet,  $4-7\mu$  broad. Uncoloured cortex  $25-40\mu$  thick, formed of (6) 8 (10) articuli, distinctly seen as a colourless layer above algal layer. Algal layer  $45-80$  ( $100$ )  $\mu$  deep, generally occupying less than one third of areolar height. Algae green, globoid,  $10-14\mu$  in diam., equally dispersed or grouped in islets. Medulla uncoloured, cells almost isodiametric,  $5-6\mu$  broad. Lower cortex dark brown or greyish violet, cells  $5-8\mu$ , nearly isodiametric, outermost 4-5 cells very dark. End cell layer uneven. Decolorate stratum absent on lower side.

Apothecia  $0.6-1.6\text{mm.}$  in diam.,  $0.2-0.35\text{mm.}$  thick. Exipulum  $60-70\mu$  thick in lateral part, black or brownish violet in outer zone, lighter inwards. K— more distinctly violet, exceptionally with brownish violet mist. Pulpa up to  $800$  ( $1000$ )  $\mu$  in diam., and up to  $300\mu$  thick, upper surface convex; brown (black), K—, J—. Paraphysogenous tissue up to  $40\mu$  thick, forming a rather continuous layer, slightly or not imbedded in pulpa. Ascogenous cells ca  $10\mu$  in diam., slightly imbedded in pulpa. Hymenium uncoloured or pale violet,  $100-135\mu$  high, J+ blue. Violet colour more distinct in K. Paraphyses loosely conglutinate, branched, septate,  $2-3\mu$  broad in lower parts,  $3-5\mu$  at apices. Epithecium brownish violet, K unaltered or distinctly violet. Asci saccate or inflated,  $80-110 \times 22-30\mu$ . Spores 2 or 1 in asci, multilocular, oblong ellipsoid ( $32$ )  $40-50$  ( $68$ )  $\times 18-32\mu$ . Young spores uncoloured, then green or violet, finally dark. Membrane  $2\mu$ ; halo  $3-4\mu$ , in K  $4-6\mu$ . (Description after material from Godhavn and Egedesminde in Greenland).

Characteristic of *Rh. Bolanderi* are the rather large and thick, often sinuate areoles with the lower side visible even when in situ on the rock;

the reddish colour (on seepages often darkened), and the often white, partially decorticated, dying areoles.

Variation. The Greenland specimens are generally larger and with a thicker thallus and larger areoles than the American, otherwise the Greenland specimens match the American ones very well. Perhaps a differentiation in the two populations will be discerned, although difficult to show up on account of the variation in both areas. In spite of the very varying spore size, the variation in the height of hymenium is the smallest in the group. Apothecia rather sparse in Greenland specimens; still not unfrequent. The f. *sulphurella* TUCKERMAN (1888, 103) not seen in Greenland.

Habitat ecology: All Greenland specimens originate from silicious rocks (Gneis, quartz, feldspar). It is a common seepage lichen, but occurs also on dryer rocks, coprically influenced by birds and dogs, as well as around human dwellings. Besides those associated species already mentioned from Sarqaaq (cf. p. 71) it occurs at Godhavn on seepages with: *Collema glebulentum*, *Crocynia arctica*, *Lecidea atrocarpoides*, *L. leucothallina*, *Lempholemma fennicum*, *L. myriococcum*, *Physcia lithotodes*, *Pyrenopsidium Iivaarense*, *Pyrenopsis pulvinata*, *Rhizocarpon badioatrum*, *Thyrea radiata*. In the often associated *Andreaea* tufts: *Caloplaca nivalis*, *Candelariella canadensis*, *Toninia squalida*. It is often snow free during winter, occasionally thinly covered by ice or snow. The rich supply of nutrition on seepages originating, not from substratum, but essentially from the irrigating water and detritus. On sandstone rocks in California the supply probably originates from dust impregnation caused by wind. It may be termed mesotrophous-eutrophous; the seepage plant in addition a seasonally hydrophilous or hydrotolerant biotype.

Distribution: N. America: In the mountains of California, Oregon, and Washington. W. Greenland: From the southermost parts northward to Upernavik (lat. 73° N.).

U.S.A.: California: Alpine co, 7000 ft., LAPHAM (*vide* TUCK.); Santa Cruz penins., Santa Cruz co: Castle rock, sandstone, 3000 ft., HERRE (Herb. MAGNUSSEN), "rare below 300 m. up to 1260 m.", HASSE (l. c.) Santa Monica Range, HASSE (247) 1903 (S); San Gabriel Range, HASSE (211), 1894 (S). Oakland: Oakland hills, BOLANDER, type; BERKELEY, 1893, 75, HOWE (H); Lassen co: Eagle lake, ad saxa silic, "Heart failure hill", BOWERMAN and CARTER 1945, (H); Oregon: No loc., CUSICK, 1882 (UPS). Washington: Loc. not given, SUKSDORF, 1882 (UPS); Yakima co: Gulch near Naches 1350 ft; Klickitat co: Bickleton, 3000 ft.; Okanogan co: Gulch near Tonasket, 1200 ft., all *vide* GRACE E. HOWARD (l. c.). Greenland: Julianehaab: Nanortalik, J. VAHL, 1829 (C); Sukkertoppen: At the harbour, 1951 (17225); Egedesminde: Arfersiorfik Fjord, Itivdliaarsuk 1951 (16022); Kuanit, 1951 (16409); Kangatsiaq, 1951 (16656, 16638); Tupilak, 1951 (16791). Christians-

haab: Sarpiussat, 1952 (19152a-b). Nugssuaq peninsula: Sarqaq, 1949 (12459). Godhavn: Lyngmarken, 1950 (12774); Lange Kær, common (15427); Arctic Station, common. Prøven: At the trading post, 1951 (field note). Upernavik: Skibshavnen, 1951 (field note); På, Orpigssuarsuit, 1951 (field note); Laksefjord, Orpít, 1951 (14617), all collected by GELTING.

### *Rhizocarpon leptolepis* ANZI

Manip. lich. rar, 1862, 29 (nomen nudum), et: Comment. soc. crittogam. Ital. I, 3, 1862, 158. ARNOLD: Lich. Fragm. 12 (Flora Regensburg. 54), 1871, 149, et in: Lich. Ausfl. Tirol. 18 et 19 (Verhdl. Zool. Bot. Gesellsch. Wien 28) 1878, 268 et 288. DALLA TORRE & SARNTH.: Flecht. Tirols, 1902, 472. VAINIO: Lich. Fenn. II (Act. Soc. Faun. Flora Fennica, 53, 1) 1922, 277 et 285. ZAHLBRUCKNER: Catal. Lich. Univ. IV, 1927, 375 et ibid. VIII, 1932, 422. RÄSÄNEN: Petsamon Jäkäläkasvisto (Anal. Bot. Soc. Zool. Bot. Fennica, Vanamo, 18, 1) 1943, 71. — *Diplozomma leptolepis* (ANZI) JATTA: Syll. lich. Ital., 1900, 428. — *Rhizocarpon amphibium* KOERBER (non TH. FR.) in: Syst. lich. Germ. 1855, 264. — *Lecidea atroalba j amphibia* NAEG. apud HEPP. Flecht. Eur. exs. no. 38. — *Lecidea atrobrunnea* NYL. (non (RAM.) SCHAEER) apud BRENNER in: Not Sälsk. Faun. Flor. Fenn. 13, 1874, 458. — *Lecidea atrobrunneola* NYL. in: Flora Regensburg. 59, 1876, 239 et apud BRENNER: Bidr. Hoglands Lafveget. (Med. Soc. Faun. Flor. Fenn. 13) 1885, 112.

Type locality: *Ad rupes micaceo-schistosas, ad dexteram torrentis juxta prata montis Sobretta praealpium Crobiarum* (N. Italy, Bormian alps), leg. M. ANZI. Ill.: HEPP. Flecht. Eur. exs. I, 1853, 38 (spores).

Exs.: HEPP. Flecht. Eur. exs. I, 38 (M. S. U.P.S.). — ANZI: Lich rar. Langobard. exs. 361. (H. M. S. O. UPS.). — ANZI: Erb. crit. Ital. 927 (M, S).

Hypothallus black, thin; edge diffuse or radiating. Septa constricted articuli dark. K—. Thallus 2–6 cm. in diam. (or larger); areoles slightly convex or subplane, round, brown to reddish brown, not shining, not pruinose; areolar margin thin, low, prominent or not, unevenly crenulate or disappearing, dark or greyish pale, not pulverulent. Lower side of areole dark, not visible in situ, narrowly fixed to substratum. Thallus K—, C—, KC—; medulla J—, K—, C—, KC—, P—.—Apothecia dispersed, adnate or sessile between the areoles. Disc black, not pruinose, finally convex and rugulose, margin thin, black, subsistent.

Areoles 0.1–0.5 mm. in diam., 0.12–0.22 mm. thick. Decolorate stratum 5–10  $\mu$  thick. Upper cortical end cells brown, 4–6  $\mu$  broad. Uncoloured cortex (5) 10 (15)  $\mu$  thick, formed of (1) 2 (3) articuli, or lacking where algae lies close to end cells. Algal layer 80–110  $\mu$  deep, occupying, in thick areoles half, in thin two thirds of areolar height, in young areoles leaving only a small zone at base free from algae. Algae green, globoid, 8–10  $\mu$  in diam., equally dispersed; grouping in islets not observed. Medulla uncoloured or greyish, cells almost isodiametric, 5–6  $\mu$ ,

forming an almost parenchymatic tissue. Lower cortex brown, cells  $4-6\mu$ ; outermost 2-3 cells dark, forming a rather thin, firm and even layer. Decolorate stratum absent on lower side.

Apothecia 0.4-0.8 mm. in diam., 0.2-0.35 mm. thick. Excipulum  $60-80\mu$  thick in lateral parts; dark brownish in outer zone, lighter inwards; K— or K+ faintly violet. End cells isodiametric,  $4-6\mu$ . Pulpa up to  $500\mu$  in diam., and up to  $200\mu$  thick; upper surface convex; brown; K—, J—. Paraphysogenous tissue forming a rather well defined layer about  $25\mu$  thick, not or slightly imbedded in pulpa. Ascogenous cells  $5-8\mu$  in diam., situated between paraphysogenous or slightly imbedded in pulpa. Hymenium uncoloured (100)  $120-140$  (150) $\mu$  high, J+ blue. Paraphyses loosely conglomerated, branched, septate,  $1.5\mu$  broad in lower,  $2.5-3\mu$  in upper part. Epithecium brown, K— or K+ violet; no mist. Asci saccate or inflated (100)  $120-140$  (150)  $\times$  (15)  $30-40\mu$ . Spores 8, multilocular, broadly ellipsoid or ovoid,  $25-32$  (37)  $\times$   $12-16$  (18) $\mu$ . Young spores uncoloured, uniseptate, old ones multilocular and often uncoloured too or finally darkened, however, always lighter than generally is the case with ripe spores in this group. Membrane  $1\mu$ , halo  $1-2\mu$ , in K broader. (Description after ANZI: Lich. rar. Langob. 361 (S. UPS)).

Characteristic of *Rh. leptolepis* are the small and thin,  $\pm$  convex, matt, reddish brown areoles with indistinct or crenulate margin, thin cortex and reduced medulla; the constantly 8, multiloculate spores, short and broad, not particularly darkened. In the herbarium specimens apothecia are generally abundant.

Variation: The Middle European population, as represented in the herbaria, varies little in outward appearance. The variations in inner structure of the areole should be further studied. The height of hymenium and size of spores varies a good deal. The medullary reaction with J according to my observations always negative even in specimens, which in the herbaria are indicated as J+. The Hogland specimens were regarded by NYLANDER as a peculiar form (f. *atrobrunneola* (NYL.) NYL.), it is, however, hardly differing from Middle European specimens. The specimens from Lapponia agree in inner structure of apothecia and areoles very well with Middle European, differ, however, somewhat in outer appearance, having almost shining, distinctly convex areoles with entire, not crenulate margin.

Habitat ecology: On silicious, steep or overhanging, often moist or shady rocks (Gneiss, granite, quartz); on seepages or on rocks along water streams. Associated with species as: *Parmelia omphalodes*, *Lecanora polytropha*, *Rhizocarpon geographicum*, *Rh. badioatrum* and *Andreaea rupe-*



*stris* incrusted by *Crocynia neglecta*. Hogland specimens from steep, bird influenced gneiss precipice with *Lecanora* cf. *subradiosa*. Lapponian specimens from gneiss and diabase.

Distribution: In the mountains of Middle Europe; mountains and lowlands of Fennoscandia.

Italy: Valesia, Alagna, quartz rocks (J—), CARESTIA, 1879 (M) — Lombardia: Bormian alps, Mt. Sobretta (type, J—) ANZI (M. S. UPS). Austria: Tirol, Oetzthal, Gurgl, am Wege zu hohen Muth (J—) ARNOLD, 1877 (M); Windischmatrei, Geschlössthale, gneiss rocks (J—) ARNOLD, 1876 (M.) Switzerland: St. Moritz (J—). HEPP & SCHAER (= Hepp. Lich. Eur. 38. M. S. UPS). Germany: Baden, Schwarzwald, Belchen. feldspar rocks (J—) MAGNUSSON & LETTAU, 1922 (Herb. MAGNUSSON, 7074). Silesia: Eulengrund (J—) 1836 (S), ex herb. v. ZWACKH, possibly first sent to KÖRBER by unknown collector. U.S.S.R.: Finlandian Gulf, Hogland, gneiss rocks (J—, acc. to NYLANDER J+) BRENNER, 1879 (H). Lapponia petsamoënsis, Parkin-antunturi (J—) RÄSÄNEN 1938 (H). Finland: Lapponia enontekiensis, Kelottijärvi, Saarenpää, diabase rocks (J—) LAURI E. KARI, 1925 (H). (According to: MAHEU GILLET Lich. de l'Est de la Corse, 1926, 88 also in Corsica. Herb. Dijon (not seen) leg. ZSCHACKE 1914).

*Rhizocarpon rittokense* (HELLB.) TH. FR.

Lich. Scand. II, 1874, 615 et in: Lich. coll. English Polar Exp. (Linn. Soc. Journ. 17) 1879, 365. VAINIO: Lich. Fenn. II (Act. Soc. Faun. Flor. Fenn. 53) 1922, 279, et 324. ZAHLBRUCKNER: Catal. Lich. Univ. IV, 1927, 341 et ibid. VIII, 1932, 425. LYNGE: Lich. Nov. Zeml. (Rep. Norw. Exp. N. Z. 1921, 43) 1928, 133 et in: Lich. W. Greenland (Medd. Grönl. 118, 8) 1937, 94 et in: Revis. Rhiz. Greenl. (Skr. Svalb. Ishav. 47) 1932, 22 et in: Bot. Canad. Arct. II (Nat. Mus. Canada Bull. 97) 1947, 322. DEGELIUS: Sydberg Kebnekaise (Bot. Not. 1945) 401. MAGNUSSON: Lich. Lycks. Lappm. (Ark. f. Bot. 33A) 1946, 82. HALE: Lich. Baffin Isl. (Americ. Midl. Natural. 51) 1954, 244. — *Buellia rittokensis* HELLBOM: Lich. ant. Lule Lappm. (Öfv. Kgl. Svensk. Vet. Akad. Förhdl. 22) 1865, 463. TH. FRIES: Lich. Spitsb. (Kgl. Svensk. Vet. Akad. Handl. 7, 2) 1867, 44. DEICHMANN BRANTH: Lich. Scoresbysund and Hold with Hope (Medd. Grönl. 18) 1894, 100. — *Catocarpon rittokense* (HELLB.) HELLB. Norrlands Lafvar. (Kgl. Svensk Vet. Akad. Handl. 20, 8) 1884, 106. — *Lecidea rittokensis*. VAINIO: Adjum. Lich. Lapp. II, 1883, 130.

Type locality: Gneiss rocks at the mountain Rittok in Lule Lappmark (Lapponia), Sweden, leg. P. J. HELLBOM, 1864 (UPS).

EXS.: NORRL. and NYL.: Herb. Lich. Fenn. 7, 1882, 345 (UPS); MAGNUSSON: Lich. select. Scand. exs. 400 (C. UPS. S).

Hypothallus black, rather thick; upper surface often cracked, white; edge mostly radiating. Septa constricted, articuli dark. K— or slightly violet. Thallus up to 15–20 cm. in diam. Areoles concave, subplane or convex, round, brown, often shining, pruinose towards margin. Areolar margin rather thick, prominent, dark, subpulverulent; when damaged and decortiated white, medulla being visible. Lower side of areole dark,



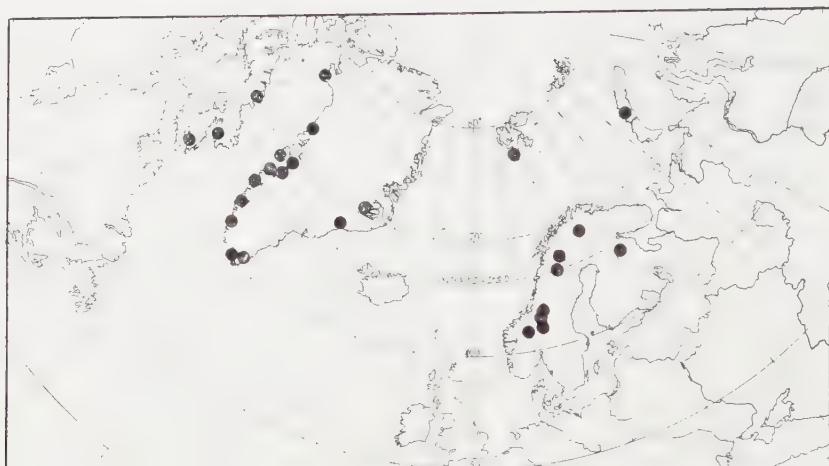


Fig. 6. Distribution of *Rhizocarpon rittkense*.

not visible in situ, rather narrowly fixed. Thallus K—, C—, KC—, medulla J— (type), P— (in aberrant types differing reactions).—Apothecia dispersed or grouped 3–5 together, adnate or sessile. Disc black, not pruinose, finally rugulose and convex; margin black, thin, subpersistent.

Areoles 0.5–1.2 (1.5) mm. in diam., 0.2–0.36 mm. thick. Decolorate stratum 20–35  $\mu$ , when old often falling off, leaving the white cortex exposed. Upper cortical end cells brown, 4–5  $\mu$  broad. Uncoloured cortex 15–20  $\mu$  thick, formed of 3–5 articuli. Algal layer 60–80 (100)  $\mu$  deep, occupying less than half areolar height. Algae green, globoid, 8–12  $\mu$ , equally dispersed or grouped islets. Medulla greyish or clear, cells almost isodiametric, 5–6  $\mu$  broad; penetrating high up into areolar margin. Lower cortex dark, cells 4–6 (8)  $\mu$ , outermost 2–3 cells very dark. End cell layer uneven. Decolorate stratum absent on lower side.

Apothecia 0.6–1.6 mm. in diam., 0.2–0.4 mm. thick. Excipulum 60–70 (100)  $\mu$  thick in lateral part; almost black in outer zone, lighter inwards. K— or K— dilute violet. Pulpa up to 600  $\mu$  or more in diam., and up to 220 (250)  $\mu$  thick; upper surface convex. K—, J—. Paraphysogenous tissue forming a diffuse, not well defined stratum at base of paraphyses. 25–40  $\mu$  thick, partly imbedded in pulpa. Ascogenous cells small, 7–8  $\mu$ , unevenly dispersed in paraphysogenous tissue or imbedded in pulpa. Hymenium uncoloured 100–140  $\mu$  high, J+ blue. Paraphyses conglomerated, branched, septate, 2  $\mu$  broad at base, 3–4 at apices. Top cell brown. Epithecium brown, K— or K+ dilute violet. Asci saccate 90–140  $\times$  25–40  $\mu$ , their lower end often imbedded in pulpa. Spores 8,

uniseptate, ellipsoid  $20-24 \times 10-15 \mu$ , when young green, later brown or black, often shrunk. Membrane  $1-1.2 \mu$ , halo  $2-3 \mu$ , in K  $3-4 \mu$ . (Description of interior after the type (UPS).

*Rh. rittokense* differs from all other species of the group by the spores being uniseptate; agrees, however, better with this group than with any other species known to me within the genus. It is the largest of the group, up to  $15-20 \text{ cm.}$  in diam. These large individuals, however, in Greenland often without apothecia.

Variation: The type has mostly concave or flattened, thin areoles, but very few convex. In Greenland convex areoles seem common, specimens with both convex and concave areoles, however, being found also. As regards inner structure and chemical reactions too, the Greenland population varies, a variation to be closer dealt with, when the material has been worked up. Quite preliminary I have alluded to this variation in the key (p. 81).

Habitat ecology: On silicious rocks (Gneiss, granite, quartz). In Greenland not found on basalt and sedimentary rocks. Here very common in gneissian areas, especially frequent on dry, wind exposed rocks, more or less snow bare in winter and dominated by *Buellietum atratae*. It also occurs, however, in more sheltered rocks, irrigated for a short time in earliest spring. Seemingly ornithocoprophobous. It may be termed mesotrophous-oligotrophous.

Distribution: Canada: Baffin Land (POLUNIN, HALE). Greenland: W. coast (VAHL, TH., FR., WARMING, KRUSE, GELTING); E. coast (HARTZ, SCHOLANDER). Spitsbergen (MALMGREN). Nowaya Zemlya (LYNGE). U.S.S.R.: E. Karelia (VAINIO). Finland: Lapponia inarense (SILÉN). Sweden: Mountains from Härjedalen in the S. to Torne Lappmark in the N. (HELLBOM, ALMQUIST, DU RIETZ, DEGELIUS, MAGNUSSON). Norway: Dovre (ZETTERSTEDT).

Of inner structural details, which may prove of taxonomic value in determining sterile specimens belonging to our group, I may mention structure of areolar margin, and upper cortex. Besides the whole picture seen in the areolar section gives good differentiating characters. The internal structure of our species further shows to which high degree they are related. As regards chemical reactions, I should like to return to this theme, when my studies on related groups of *Rhizocarpon* are more advanced.

Standing at the rock at Sarqaa (cf. p. 71) I took the areoles of one of the species to be apothecia. It was not the failing light alone, which caused this mistake. Other lichenologists seem to have had the same experience. Thus KÖRBER (1855, 264) compare the areoles of *Rh. leptolepis*

with lecanoroid apothecia, and on the label of the first collection of *Rh. Bolanderi* possibly ever made, that of JENS VAHL, 1829, from Nanortalik in southernmost Greenland, we find in the manuscript of DEICHMANN BRANTH: "Squamulae sunt thallinae, non apothecia". It should, however be remembered, that the areoles in outer appearance are similar, not to the apothecia of the group, but to lecanorine apothecia. The possibility of misinterpretation exists thus only in sterile specimens and for persons not yet acquainted with the group.

The apothecia of the group are in outer appearance not very similar to the areoles, internally, however, there are striking analogies as seen from the following scheme:

Areoles	Apothecia
Lower Cortex.	Excipulum.
Medulla.	Pulpa.
Upper cortex.	Paraphyses.

If we add to this, that both areoles and the uniplontic parts of the apothecia are differentiated from hypothallus, we may indeed admit the truth of the words of FRIES (Lich. Eur. Ref. 1831, LXIII): "Apothecia repetunt intra angustiores limites organa elementaria thalli, sed magis nobilitata et definita."

### Literature.

- FINK, BRUCE, 1935: The lichen flora of the United States. — Ann Arbor, Mich.  
 FRIES, ELIAS, 1831: Lichenographia Europaea reformata. — Lundae.  
 FRIES, TH. M., 1874: Lichenographia Scandinavica. II. — Upsaliae.  
 GALLØE, OLAF, 1927–54: Natural History of the Danish Lichens. København.  
 Part I, 1927. Part II, 1929. Part III, 1930. Part IV, 1932. Part V, 1936. Part VI, 1939. Part VII, 1948. Part VIII, 1950. Part IX, 1954.  
 HOWARD, GRACE E., 1950: The Lichens of the State of Washington. Seattle.  
 HALE, JOE, jr., 1954: The Lichens of Baffin Island. — Americ. Midland Naturalist, 51.  
 KÖRBER, G. W., 1855: Systema Lichenum Germaniae. — Breslau.  
 LYNGE, B., 1932: A Revision of the Genus *Rhizocarpon* in Greenland. — Skr. Svalb. og Ishavet 47.  
 MAGNUSSON, A. H., 1952: Lichens from Torne Lappmark. — Ark. f. Bot. ser. 2. Bd. 2. 2.  
 NANNFELDT, J. A., 1932: Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten. — Nova Acta Reg. Soc. Sci. Upsal. Ser. IV. 8, 2.  
 TUCKERMAN, E., 1872: Genera lichenum. — Amherst, Mass.  
 VAINIO, E. A., 1922: Lichenographia Fennica II. — Act. Soc. Faun. Flora Fennica, 53, 1.

## The Lifeform and Growth of *Artemisia campestris* L.

By K. GRAM

In Denmark *Artemisia campestris* is considered to be either a hemi-cryptophyte or a chamaephyte (RAUNKIÆR, 1950, WARMING, 1909). In England it is called a subshrub or chamaephyte (CLAPHAM et al., 1952). From Germany it is described as a "Halbstrauch oder Horststaude" (HEGI).

In some grey dunes of Northeast Sealand the author has made some observations on this plant and has at an earlier occasion (1951) briefly dealt with some of these in Danish. Fig. 1 is taken from this book and shows a typical many-headed root ("mangehovedet rod, radix multiceps", WARMING, 1884). As the lower, surviving parts of the branches are lignified it seems quite natural to call the Field-Southernwood a subshrub or a chamaephyte, but as far as the author has seen the only buds that for certain can be expected to survive are those placed just in the soil-surface. After an extremely mild winter (as f. i. 1952/53) some of the upper (chamaephytic) buds will flush, mostly producing weak shoots that do not amount to anything. After normal Danish winters and naturally after the more severe winters too, only buds from the surface of the soil (hemicryptophytic buds) will produce new assimilating and flowering shoots.

It seems very probable that *Artemisia campestris* subsp. *eucampestris* BRIQ. & CAV. with which we are dealing here in Denmark and adjacent countries, may survive as a typical chamaephyte in climates having a milder or eventually a more stable winter.

Among 187 young plants (1-4 years old) investigated in 1950 the most common type (60 % or 112 plants in all) must have started like that shown in Fig. 2. These types were found on soil without moss-layer and not influenced by drifting sand. Such a plant may develop into a specimen





Fig. 1. *Artemisia campestris*; about 10 years old plant seen from below. (rnot. S. FRANCK).



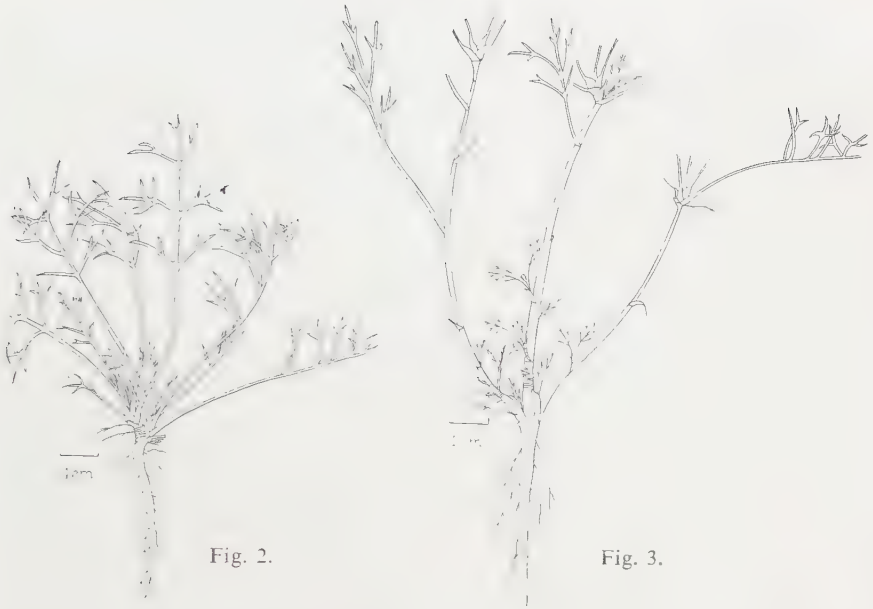


Fig. 2.

Fig. 3.

Fig. 2. *Artemisia campestris*; 1 year old plant; the most common type. – Fig. 3. *Artemisia campestris*; 1 year old plant from shade between high grasses. Most of the leaf-blades omitted.

like that of Fig. 1 if a slight elevation of the soil-surface will take place in the course of the years.

Specimens like that drawn in Fig. 3 are rather seldom met with (in all 11 i. e. 6 % were seen); they have more or less upright branches ending each in a rosette of leaves, that next year may produce either a vegetative or a flowering shoot when laid down and hidden in the moss-layer or the litter of the vegetation; if this does not happen they will only be able to survive if the winter should turn out to be extraordinary favourable. The scars of the rosette-leaves from the first season show that rosette-buds have survived here just below the surface of the moss-layer and sheltered by it. In severe winters, especially those with frosts without snow, these buds are killed. This shows clearly some chamaephytic features in the nature of our plant but too that in the Danish climate the hemicryptophytic buds are the only being quite winter-proof.

To a certain degree nearly  $\frac{1}{3}$  (33 %) of the investigated plants behaved like that illustrated in Fig. 4 having one to several procumbent shoots each producing a terminal rosette and often some lateral, minor ones too. Very seldom (only seen 9 times among the 62 investigated plants of this type) a few tiny, adventitious roots, as shown in the drawing, may occur.

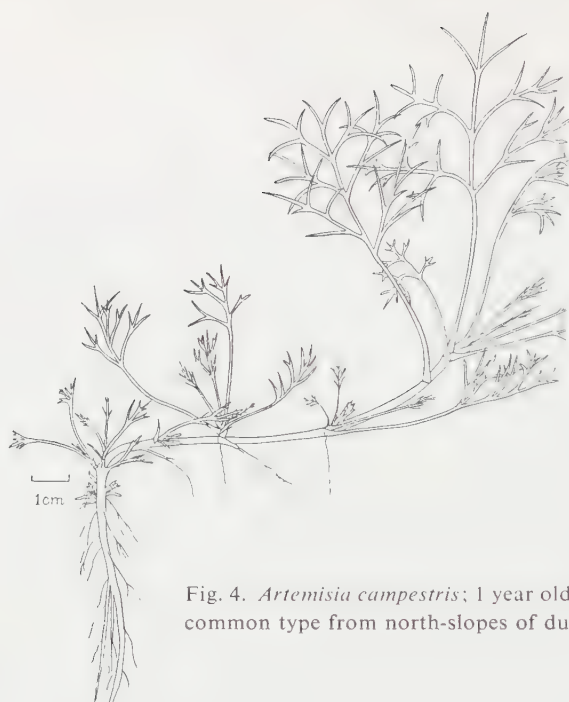


Fig. 4. *Artemisia campestris*; 1 year old plant; rather common type from north-slopes of dunes.



Fig. 5. *Artemisia campestris*; 4 years old; very rare type with stolons growing in a thick layer of moss on north-slopes of dunes. A. rosette 1946-47. B. dead shoot from 1948. C. rosette 1947-48. D. rosette 1948-49 (dead). E. rosette 1949-50. F. rosette 1950-51. G. flowering shoot 1948? H. flowering shoot 1949. I. flowering shoot 1950. Nearly all leaf-blades and many details omitted.

During the winter the specimen has suffered from a covering by a stratum of about 1 cm. drift-sand. Most of the buds from the immersed part of the stem may in the autumn or next year develop into new rosettes and thus participate in forming a many-headed root and the aspect—in this case quite false—of a chamaephyte. Molehills as a matter of fact often are the cause of the same effect.

Finally Fig. 5 shows a case that only has been met with two times. It has grown in a very thick layer of moss and has been object to a slight covering by drift-sand. Two of the rosettes (C and E) have managed to produce an adventitious root developing into a true, but weak and short taproot, thus giving the creeping stems the character of stolons. This seems to take place very rarely, and more seldom yet it leads to vegetative propagation on account of the uneffectiveness of the new taproots, but if one day or another a strain may produce better adventitious taproots we will have another troublesome weed.

### Summary.

*Artemisia campestris* L. subsp. *eu-campestris* is a perennial with a many-headed root (Fig. 1) and is in Denmark a hemicryptophyte. The influence of drifting sand, moss-vegetation and shade on the stretching of the rosette-shoots is demonstrated (Figs. 2–4), and in Fig. 5 an attempt to vegetative propagation by stolons is seen. This case was only found in two plants of 187 more thoroughly investigated in 1950 and never found since.

### Literature.

- CLAPHAM, A. R., TUTIN and WARBURG, 1952: Flora of the British Isles, p. 1088. Cambridge.
- GRAM, K. & JESSEN, 1951: Vilde planter i Norden, 2 ed., 4: 1377–1381. København.
- HEGL, G.: Illustrierte Flora von Mitteleuropa, 4, 2: 666. München.
- RAUNKJÆR, C., 1950: Dansk Ekskursionsflora, 7th ed. by K. Wiinstedt, p. 310. København.
- WARMING, E., 1884: Om Skudbygning, Overvintring og Fornylelse. Den Naturhistoriske Forenings Festskrift 1: 23.
- E., 1909: Dansk Plantevækst, 2. Klitterne, p. 295. København.

## *Galium boreale* L., New to Greenland

By JOHS. GRÖNTVED

Last year (1953) I had the opportunity to make a journey to South Greenland, to the Julianehaab district, already visited by me in 1937. The Carlsberg Foundation granted the necessary funds for the journey. As the Forest Planting Expedition under the leadership of professor C. A. JØRGENSEN from the Agricultural Highschool, Copenhagen, was also going to Greenland, I was kindly invited to join the party. I am very much indebted to professor C. A. JØRGENSEN for this kindness.

During my stay in Greenland, from May 21th to August 6th, I visited various places in Tunugdliarfik Fjord; most time, though, was spent in the vicinity of the sheep breeding station at Upernaviarssuk at the mouth of the Igaliko Fjord.

One of our temporary stations were at Qanasiarssat, a locality situated some 3 km. from the head of Tunugdliarfik Fjord, on its eastern shore. On June 11th I made an excursion from this station to Qingua (the head of the fjord). About one km. north of Qanasiarssat I came across a patch grown with *Galium boreale*. The locality was situated on a gentle slope just on the steep brink along the shore; it had a growth of low and somewhat scattered bushes of *Salix glauca* and *Betula contorta*, and *Galium boreale* was forming a dense green carpet over some few square metres. The plants were then only 4–5 cm. high. As I reckoned that I might have an opportunity to visit the place later on, I did not take any specimens for the herbarium.

On July 10th our party again visited Qanasiarssat, and this time I had the good luck to find *Galium* in full flower. The plants then averaged 10–15 cm. of highth, some few, though, measured up to 30 cm., and it may be supposed that, when fully developed, most of them would reach this height. As our party stayed only for some few hours at Qanasiarssat, I did not have time enough left for a more thorough investigation of the locality.



Fig. 1. *Galium boreale* L. from Tunugdliarfik Fjord, 1953 (left) and from Úlfarsfell S. W. Iceland, 19. VII. 1947 (right). Nearly natural size.



It is a well known fact that *G. boreale* is a very variable species (cfr. e. g. FERNALD 1928), p. 106, and HULTÉN (1949), p. 1434.) In FERNALD: Gray's Manual of Botany, 1950, p. 1322–23, the following 3 varieties are described as follows:

Fruit hairy

Fruit villous-hirsute with long hairs. . . . . *G. boreale* var. *typicum* BECK

Fruit covered with appressed or incurving hairs . . . . . var. *intermedium* DC.

Fruit glabrous or glabrate . . . . . var. *hyssopifolium* (HORNEM.) DC.

According to this key, the Greenland specimens can undoubtedly be referred in the var. *typicum* BECK.

The geographical area of *G. boreale* coll. is as follows: Europe: from Iceland, Great Britain, Scandinavia (from Nordkap), Kola peninsula, and northern Ural, south to the Pyrenees, isolated area in Central Spain, Northern Italia, Thracia, Caucasus and Armenia; in Switzerland (Wallis and Engadin) it ascends to 2200 m. alt. America: from Quebec to Alaska (Yukon and Mackenzie delta), south to N. California, Colorado, New Mexico, Nebraska, Missouri, Michigan and Pennsylvania and New Jersey. It is even mentioned as the most common *Galium* in Canada. Asia: from the Obj river (67° N. lat.), from Jenisei (ca. 70 N. lat.), from the lower Lena river and Chukch peninsula, south to Mongolia, N. Corea and Yeso.

It may be added here that all three above named varieties occur in N. America and in Eurasia. In N. America the var. *typicum* is found chiefly in the Northwest, from Manitoba and through the western states; only very few (3) localities are known east of Manitoba (FERNALD (1928), p. 107). The var. *typicum* is the common form in Iceland, and this might suggest, that the Greenlandic *G. boreale* has come from the East. In which way it may have reached SW-Greenland can, however, scarcely be decided with any acceptable certainty. It is now to be looked upon as unquestionably belonging in the Greenland flora. Future investigations must decide whether *G. boreale* may possibly be found in other localities in SW-Greenland.

It may seem rather curious that this species has not been observed previously, as the locality at Qanasiarssat is situated in the immediate neighbourhood of the footpath to Qingua, and no doubt several botanists have passed near by these last fifty years. The distance from Qanasiarssat where, at the beginning of this century, Professor KOLDERUP ROSENVINGE

planted a small group of *Pinus silvestris* and *Picea Abies*, is only about one km. There is however, scarcely any reason to suppose that *G. boreale* was introduced together with the young trees planted by ROSENVINGE.

The genus *Galium* is represented in Greenland by the following five species: *G. Aparine*, *G. boreale*, *G. Brandegei*, *G. triflorum*, and *G. uliginosum*. *G. Aparine* and *G. uliginosum*, though, have been found only as accidentally introduced.

*G. Aparine* L. was found by N. HARTZ in a garden at Ritenbenk, 69° 44' N. lat. The specimens taken in September 1890 were near flowering. Flowering specimens were found by me in a garden at Godhavn, Disko, on September 2nd, 1932, and this species is also recorded as found by J. AUG. BERLIN, as "introduced in a garden at Ivigtût" (1883?), cfr. JOH. LANGE, 1887, p. 269.

*Galium Brandegei* GRAY is known from numerous localities in W-Greenland between 60°10' N. lat. and 64°20' N. lat. In East Greenland it has been collected by CHR. KRUSE in 1902 at Tasiussak in Angmagsalik district at 65°37' N. lat. (KRUSE (1906), p. 255). The geographical area of this species is: Greenland, Labrador (to 58° N. lat.) to Alaska, south to Newfoundland, Quebec, Great Lakes and Maine, California, Arizona and New Mexico. In Europe it has until now, as far as known, been recorded from Iceland only (GRÖNTVED, 1942, p. 352). Cfr. also HULTÉN, 1949, p. 1436.

*G. triflorum* MICHX. is known in W.-Greenland between 60°16' N. l. and 61°15' N. l. Moreover has been, collected (ca. 1823) by C. P. HOLBØLL at Fiskeræset at 64°10' N. lat. From East Greenland it is recorded by DEVOLD & SCHOLANDER (1933, p. 93) from 60°35' N. lat., and from 62°40' N. lat. The geographical area is: Greenland, Newfoundland to Alaska, south through eastern Canada and the northern states, reaching Virginia, Tennessee, Louisiana, Texas and Mexico. Europe, from northern Scandinavia to southern Sweden, Estonia, Central Russia, and isolated areas in the Alps.—Asia, in the W. Tobolsk province and N. Tomsk prov., at upper Jenisei river, and Jakutsk distr. Kamtchatka. From Saghalin, Ussuri, Central Kuriles, Corea and Kyushiu a very closely related species, *G. trifloriforme* KOM. is recorded (HULTÉN (1949), p. 1441).

*Galium uliginosum* L. was found by me on September 14th, 1937, in the Colony Ivigtût (61°13' N. lat.) on a refuse heap, and among *Salix* shrubs near a house in the colony, September 17th. On the last mentioned locality the individuals measured up to 45 cm., and were copiously flowering.

Finally it deserves notice that *G. pumilum* MURR. (*G. silvestre* POLL.) which is one of the most common plants in Iceland, has not yet been observed in Greenland.

### Literature.

- BÖCHER, T. W., 1938: Biological Distributional Types in the Flora of Greenland. – Medd. om Grønland. 106
- DEVOLD, J. and SCHOLANDER, P. F., 1933: Flowering Plants and Ferns of Southeast Greenland. – Skrifter om Svalbard og Ishavet. 56. Oslo.
- FERNALD, M. L., 1928: The Varieties of *Galium boreale*. – *Rhodora*. 30.
- 1950: Gray's Manual of Botany. Eighth Ed. Boston.
- GRÖNTVED, JOHS., 1937: Additions to the Flora of South West Greenland. – Botanisk Tidsskrift. 44.
- 1942: The Pteridophyta and Spermatophyta of Iceland. – Botany of Iceland, Vol. IV, Part I. Copenhagen.
- HULTÉN, ERIC, 1949: Flora of Alaska and Yukon. – Lunds Universitets Årsskrift. N. F. Avd. 2. 45, 1.
- KRUUSE, CHR., 1906: List of Phanerogams and Vascular Cryptogams found in the Angmagssalik District on the East coast of Greenland between 65°30' and 66°20' lat. N. – Medd. om Grønland. 30.
- LANGE, JOHS., 1880: Conspectus Florae Groenlandicae. – Medd. om Grønland 3.
- 1887: Conspectus Florae Groenlandicae. Pars secunda. København.
- ROSENVINGE, L. KOLDERUP, 1892: Andet Tillæg til Grønlands Fanerogamer og Karsporeplanter. – Medd. om Grønland. 3.

# Autogamy in some Drooping *Bicornes* Flowers

By O. HAGERUP

## 1. Introduction.

Fertilisation in *Bicornes* is a favourite example of ingenious adaptation of entomogamy. The proboscis of visiting bees is generally supposed to strike the horns of the anthers, thereby shaking pollen down over the insects. From KNUTH's manual these views spread to manuals and textbooks of flower biology all over the world even though it was suggested already by WARMING that certain species could also be autogamous.

Through observations in Nature I, too, came to question the acceptability of the classic views on entomogamy in *Bicornes*, especially when I had made various travels in arctic regions where there are no or very few pollinating insects and where the flowers of *Bicornes* are nevertheless capable of developing plenty of fruits.

This is particularly in evidence in the Faroe Islands where I examined *Vaccinium uliginosum* in localities where there were no chance of visits by bumble-bees, bees, ants, butterflies or other pollinators and yet all the flowers were pollinated and developed fruits.

In the rough east coast of Greenland (at latitude 71° N.) *Vaccinium uliginosum* var. *microphyllum* forms enormous growths covering large areas. In this region this plant develops such quantities of fruits that in the latter part of the summer they constitute the main source of nourishment for numerous birds and mammals. Even the big polar bears can get enough food by gathering the many small berries that colour the excrements of these animals. There are so few bumble-bees and small butterflies that they only can manage to visit a small fraction of the millions of flowers growing there, but the flowers nearly always bear fruit without relying on the chance of casual visit by an insect. That applies also to *Cassiope tetragona*: quantitatively, visits by insects are insignificant.

Hence there is scarcely any reason to doubt that these flowers can be fertilized in ways that are entirely different from those assumed by the classic flower biologists. In order to elucidate the fertilization process some species were examined in Nature and in The Botanical Garden in Copenhagen. The flowers were covered by bags which prevented visits by insects. Series of microtomic sections were examined and revealed remarkable structural conditions which could not have been detected with the more primitive technique available to the older investigators.

## 2. *Vacciniaceae*.

### *Vaccinium uliginosum*. Figs. 1 and 15.

This flower has been well described, for instance by WARMING (1908, pp. 47–48). I therefore only present a drawing (Fig. 1) of a median, longitudinal section of the flower (self-fertilized in a bag), showing several hitherto unnoticed structural features of the stamens. It will be seen that the stamen has a very thin basal part permitting the stamen to move inwards toward the style. This movement is effected by pressure from the corolla on which there is a ring-shaped pad just above the base. The pad is held tightly against the stamen which has a big bulge facing the pad of the corolla. At its distal end the stamen is again very thin permitting the anther to move inwards toward the style.

The structure of the anther is also very remarkable. At its distal end it is drawn out into a long tube which is so narrow that only a few tetrads of pollen can pass it at a time. At the tip of this tube the opening of the anther is pressed tightly against the style. On each anther are the two well-known horns after which the order was named. Most of the existing numerous drawings of these horns are wrong in that they show the ends of the horns to be unattached in the cavity of the corolla. In *V. uliginosum* the horns are firmly pressed towards the inside of the corolla like tense springs holding the anther against the style and above the stigma.

The style, too, is remarkable in having at its centre a cavity with a star-shaped cross-section (Fig. 14). During the flowering the stigma is covered by a large lump of mucilage in which the pollen will germinate quickly and send pollen-tubes down through the canal of the style where they are fairly easy to recognize in sections.

When the corolla withers and loosens at the base, the stamens, being fastened to the corolla at their bases, will come off too; the anthers will often stick to the mucilage on the stigma (cf. Figs. 5, 6, and 8).

The flower has a slight fragrance and the upper surface of the ovary





Fig. 1.



Fig. 2.



Fig. 3.

Fig. 1. *Vaccinium uliginosum*. Longitudinal section of flower, self-pollinated in bag. ( $\times 11$ ). – Fig. 2. *Vaccinium myrtillus*. Longitudinal section of flower, self-pollinated in bag. ( $\times 9$ ). – Fig. 3. *Oxycoccus palustris*. Flower. ( $\times 6$ ).

secretes nectar; yet there are remarkably few insect visits, although KNUTH gives a rather long list of visiting insects from more southern localities; in Denmark I have only seen a few flies (*Eristalis*) on the flowers and quantitatively insect visits are of no importance in Northern Europe.

In order to study the problems of pollination flower-buds were wrapped into bags to keep insects out. In a few weeks it was found that all the flowers were powdered by pollen, both on the inside of the corolla, on the style, and on the stigma. Microscopic examinations revealed that the pollen had germinated, sending long pollentubes down through the canal of the style. Later, fruits began to develop.

In order to ascertain the part played by the wind in the pollination flowers were placed under glass in compartments where they could not be reached by the wind. In this case no pollen came from the anthers and the flowers were consequently not pollinated. Microscopic examinations showed that the anthers were full of pollen. Hence, the pollen can only get out through the narrow cannula of the anthers when the flower is constantly shaken by the wind. The mechanism resembles a pepper-box which gives off its contents through narrow pores, but only when it is constantly shaken.

Even in open air some pollen still remain in the anthers, because the passage out of the anthers is so difficult. The importance of wind to

autogamy is also brought out by the fact that plants sheltered from the wind, for instance by being surrounded by trees, develop comparatively few fruits, whereas fruition is abundant in completely open country such as the heaths of northern Greenland.

*Vaccinium myrtillus*. Fig. 2.

Most of the details given above on *V. uliginosum* also apply to *V. myrtillus*. Both have a very weak flow of pollen falling slowly from the narrow openings of the anthers along the style and on to the stigma. The corolla of *V. myrtillus* has a comparatively narrow opening which it is difficult for pollen to pass without touching the stigma at the entrance to the flower.

The opening of the anthers is just above the stigma, because the anthers are mutually accrete. They unite already in the bud when the horns press them tightly together and inwards against the style. In the full-blown flower the horns do not touch the corolla and may therefore be shaken by insects.

In Denmark insect visits are common. Both bumble-bees and honey-bees often visit the flowers. Frequently the openings are enlarged by bites of ants which then crawl down to the nectary.

However, the flower's own flow of pollen begins at the time when the corolla opens. Generally, the flower has thus been fertilized, before insects bring pollen from outside. In arctic districts where the plant is not fertilized by insects, fruits develop all the same. That the species is not always autogamous will be seen from the fact that it forms a hybrid with *V. vitis idaea*.

The stigma is pollinated even if insects are shut out by tying bags round the flowers. When the corollas fall off the stamens come off too. As they remain in their original position fastened to the corolla, they deposit pollen direct on the stigma. The flow of falling pollen may easily be controlled by placing a glass plate or a piece of paper just beneath the entrance to the corolla. If the wind is shut out so that it cannot shake the flower, all the pollen will remain in the stamen.

The wind carries the pollen coming from the narrow mouth of the corolla; the latter is only partly closed by the large stopper of mucilage of the stigma, but the chance of anemogamy is comparatively slight because the stigma is inside the corolla. Sometimes, however, there is a little pollen at the outside of the corolla. The "Anemo-autogamy" is very effective, so that almost all flowers are fertilized.

*Vaccinium vitis idaea.*

The morphology and biology of this flower resembles those of the two previous species, but the opening of the corolla is larger (cf. WARMING, p. 51); besides, the style protudes some way of flower and this means an additional chance of anemogamy and comparatively fewer chances of autogamy. Moreover, the flower is visited frequently by insects and may probably also be entomogamous although it bears fruits in quantities that make it worthwhile to gather these in districts of Greenland where there are few insects.

If the flowers are covered by bags pollen may nevertheless be found everywhere in the interior of the flower and on the stigma. The falling pollen is easy to collect on a piece of paper. Anemoautogamy is apparently both the most frequent and the safest method of fertilization. Since the flowers are close to each other the light pollen may easily be carried by the wind from one flower to another. In some flowers there were *Trips* which may cause both autogamy and entomogamy.

*Oxycoccus palustris.* Fig. 3.

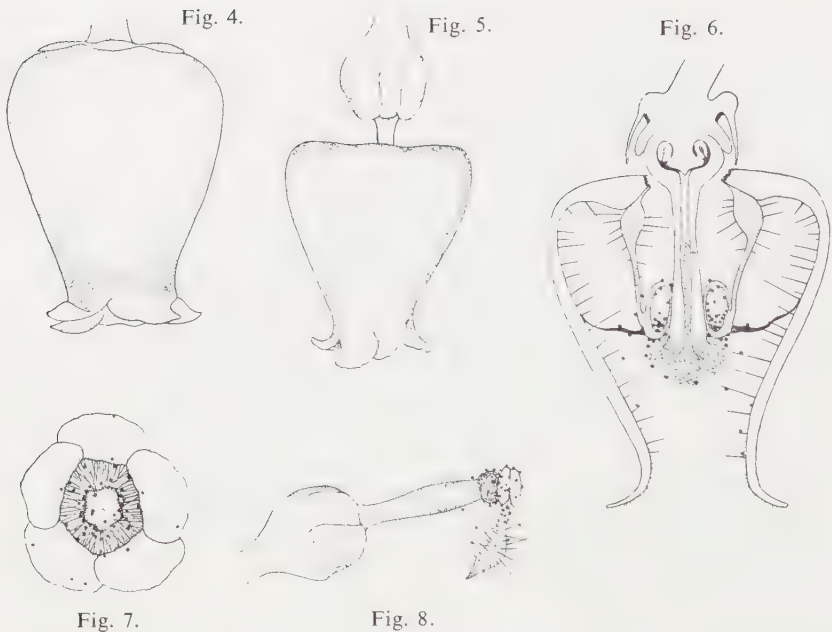
This plant differs from the previous species in that the corolla is completely open, permitting the wind to carry the pollen away as soon as it has left the anthers. The long style also indicates anemogamy.

KNUTH stated that insect visits are very rare in more southern localities. In Denmark, however, I have for several years noticed very numerous visits of honey-bees and bumble-bees flying from flower to flower so that they could not help fertilizing them. However, fruits also develop in arctic districts with few insects and if flowers are closed off in bags they will be fertilized if shaken by the wind. Under glass no pollen comes out of the anthers and in any case little pollen is found on the stigma.

As in the previous species of *Vaccinium*, anemo-autogamy is found to be the most frequent and certain method of fertilization in *Oxycoccus*. Anemogamy and entomogamy also occur occasionally.

3. *Ericaceae.*

In the majority of *Ericaceae* the fertilization is similar to that described above for *Vacciniaceae*. As WARMING gave a good description of the flowers, only a few supplementary drawings are given here. In most species the stamens are surrounded by a tightly fitting corolla, which prevents the wind from removing the light pollen before the latter passed the narrow mouth of the corolla near to the stigma. The structure of the



Figs. 4-8. *Arctostaphylos uva ursi*.

Fig. 4. Flower; sepals patent. ( $\times 9$ ). – Fig. 5. Corolla has come off halfway. ( $\times 8$ ). Fig. 6. Longitudinal section of flower with falling corolla. The stigma is caught by the stamens that fertilize it. ( $\times 10$ ). – Fig. 7. Opening of a self-pollinated flower. ( $\times 16$ ). – Fig. 8. Withered flower; one stamen is kept by the stigma. ( $\times 8$ ). For further details, see the text.

stamens is also remarkable and they are situated just above the stigma, thereby ensuring autogamy.

*Arctostaphylos uva ursi*. Figs. 4-8.

The structure of the stamens (Fig. 6) is the same as in *Vaccinium*: they have a slender hinge at the base; immediately above it, a big bulge is tightly pressed against a circular pad situated along the base of the corolla opposite the bulge. This pressure forces the stamens away from the corolla towards the style. The horns of the stamens press the latter towards the style so that they become situated immediately above the stigma, which is covered by a large lump of mucilage.

The corolla and the stamens open up at the same time; the pollen grains are then discharged singly down towards the stigma; the risk of missing it (thus losing the pollen outside the flower) is slight, not only because the mouth of the corolla is narrow, but also because the inside

of the corolla is densely covered with stiff hairs on which the pollen-grains falling farthest from the stigma remain temporarily suspended; they are later shaken free by the wind and continue their fall down towards the stigma.

The flower is normally fertilized in the gentle flow of falling pollen. In addition, the flower has a remarkable ultimate, but safe, method of pollination, which HCEG was the first to find in *Cassiope tetragona*:

During the flowering (Fig. 4) the calyx is horizontally patent, but when the corolla begins to wither the sepals bend upwards (Fig. 5) with great force, swelling heavily at their base. This pressure against the bottom of the corolla makes it burst and come off it at its base; then the corolla and the stamens fastened to it slide down along the style until they hit the stigma. In many cases the anthers get stuck in the mucilage on the stigma and the peculiar situation occurs which is illustrated in Fig. 5: the corolla falls only half-way down the style where it stops. At last the wind shakes off the withered corolla, but sometimes a few stamens may remain on the musilage of the stigma (Fig. 8). There is always some pollen left both inside and outside the anthers and some of that pollen will fertilize the flower, if the other methods of pollination have failed.

This remarkable form of autogamy may occasionally be observed in most Danish *Bicornes* whose stamens are fastened to the corolla. Even when the withering corolla does not get stuck halfway, the anthers with the pollen lying on them will rub against the mucilage on the stigma.

In open air numerous flowers were kept in bags; although insect visits were thus cut off, the interior of the flowers was powdered with pollen, and the fruits had started growing. If the wind is prevented from shaking the flower by placing the latter under a glass dome, no pollination will take place until somebody shakes the flowers.

Insect visits have also been observed (KNUTH), but the animals generally come too late to fertilize the flower because the pollen begins to fall as soon as the flower starts opening.

As the stigma does not protrude outside the corolla, the possibility of anemogamy is extremely slight.

The plant also fructifies in arctic regions where the possibility of entomogamy is negligible.

#### *Andromeda polifolia*. Fig. 16.

The morphology and biology of this species is closely related to the previous one. At their base the stamens are tightly fixed between the





Fig. 9.



Fig. 10.



Fig. 11.

Fig. 9. *Arctystaphylos alpina*. Longitudinal section of flower-bud in autogamy. ( $\times 15$ ). – Fig. 10. *Erica carnea*. Longitudinal section of flower; anemogamy. ( $\times 11$ ). – Fig. 11. *Erica mediterranea*. Anemogamy. ( $\times 10$ ).

corolla and the ovary and the horns of the anthers lean firmly against the corolla, the stiff hairs of which prevent the horns from sliding out sideways, even if they happen to be touched by an insect.

The entrance of the corolla is almost completely closed by the stigma, which is covered by a large lump of mucilage. The free passage beside the stigma is nearly blocked by stiff hairs on the inside of the corolla.

As soon as the flower opens, the pollen, too, immediately begins to fall down on to the stigma; this may even happen a little before the flowering (bud-autogamy). Insects, if any, will therefore generally be too late to fertilize the flower. The stigma is seated too deep in the corolla for the anemogamy to be of any importance.

In open air all flowers are pollinated abundantly, even if they are covered with a bag, but in compartments closed off from the wind no pollination takes place.

The stamens are fastened to the corolla; when the latter falls off it will often remain hanging on the middle of the style; in such cases autogamy occurs as shown in Figs. 5–6.

In autogamy the pollen germinates immediately, the pollen tubes penetrating down through the canal of the style where they may easily be seen.

*Arctostaphylos alpina*. Fig. 9.

This species represents a form of autogamy which is different from the previous ones: the anthers open before the corolla and the pollen immediately falls downwards and accumulates at the hairy tips of the petals at the very place where the viscous stigma is found as a sticky stopper which is filled with the plant's own pollen, before the flower comes out. Hence, the very few arctic insects are generally too late to pollinate the flower. Anemogamy, too, is difficult and superfluous. Incidentally, reference is made to WARMING (pp. 34-38), who also mentioned autogamy.

In the canal of the style numerous pollen tubes were found, developed by the plant's own pollen.

*Phyllodoce coerulea*. Fig. 12.

The existing descriptions (WARMING, pp. 17-22) will only be supplemented here by a median longitudinal section showing that in the usual way the long stiff stamens are pressed firmly on at the base, thereby being forced towards the style so that the anthers are situated just above the viscous stigma. As in *Arctostaphylos alpina*, the slow flow of falling pollen begins almost at the time when the corolla opens or slightly earlier and goes on during the whole flowering season. After this bud-autogamy there are numerous pollen tubes in the canal of the style. The fructification is abundant in arctic regions, where the possibility of insect visits is negligible.

In the Botanical Garden in Copenhagen there were numerous *Thrips* in the flowers. The eggs of these small insects were found in the wall of the ovary and in the style, but not in the falling corolla. These animals ought to be searched for in Nature.

As the style does not protrude from the corolla, there is scarcely any possibility of anemogamy.

*Cassiope tetragona*. Figs. 13, 14.

This well-described arctic species (WARMING, pp. 27-28, and HOEG) I saw as a mass vegetation at latitude 71° N. on the coast of East Greenland; there it was remarkable that most of the fading corollas remained hanging on the middle of the style (cf. Fig. 6), where they were found dangling in the wind so that the remarkable autogamy (shown in Figs. 5 and 6) was inevitable.

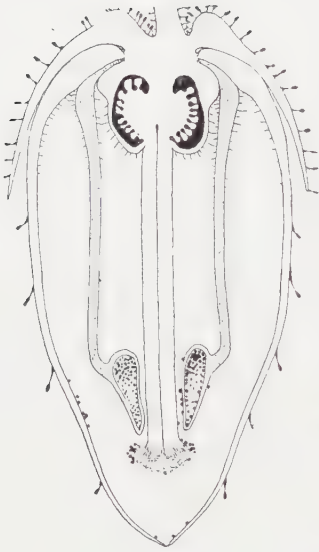


Fig. 12.

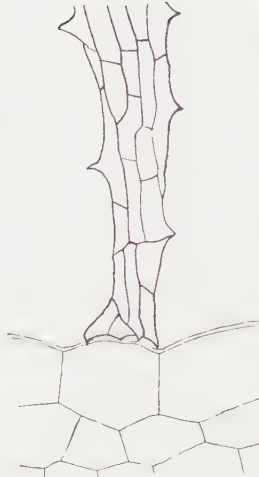


Fig. 13.

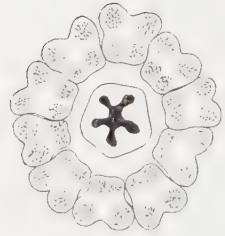


Fig. 14.



Fig. 15.

Fig. 12. *Phyllodoce coerulea*. Longitudinal section of bud in autogamy. ( $\times 13$ ). – Fig. 13. *Cassiope tetragona*. Tip of horn leaning firmly against the inside of the corolla. ( $\times 360$ ). – Fig. 14. *Cassiope tetragona*. Cross section of the tubular, accrete stamens surrounding the style. ( $\times 35$ ). – Fig. 15. *Vaccinium uliginosum*. Pollen germinated after autogamy. ( $\times 300$ ).

The plant also has bud-autogamy, the pollen beginning to flow before the flower has opened; pollen tubes will then soon be found in the canal of the style.

The base of the stamens is very tightly fixed in the usual way between the corolla and the ovary. The horns of the anthers lie very tightly against the inside of the corolla (Fig. 13); therefore, the anthers are pressed so hard together that they surround the style like a tube (Fig. 14) in a way similar to the majority of the *Bicornes* mentioned above. The stigma is situated at the centre of the flow of falling pollen.

Bumble-bees rarely visit the fragrant flowers, which at that time have already been pollinated.

*C. hypnoides* also has bud-autogamy (WARMING, p. 24); consequently, it is certain to bear fruits in the extreme north where insects are scarce. Similar conditions also exist for *Erica cinerea* in the Faroe Islands (HAGERUP, 1951, p. 19.)

*Erica carnea* (Fig. 10) and *Erica mediterranea* (Fig. 11).

In the foregoing species anemogamy was of little or no importance. However, it is a well-known fact that *Calluna* as well as other species may be pollinated by the wind while being entomogamous at the same time. This applies to many southern species such as *E. carnea*, which in Denmark is amply visited by bees as well as bumble-bees. However, clouds of pollen are also thrown into the air when the flower is shaken. Such flying pollen first hits the long style protruding from the same flower and then other flowers standing near to it. (KNUTH is of the opinion that it is a butterfly flower and that autogamy is impossible). If the plants are cultivated under glass, however, they will be pollinated if they are shaken (for instance during watering).

The tips of the anthers with their openings reach outside the flowers; the pollen will thus easily get out into the wind. Therefore, there is always plenty of pollen on the stigmas, although the latter are very narrow.

Studies of plants in herbaria showed that in numerous other species of *Erica* (for instance from South Africa) all the anthers are pressed tightly together in the narrow entrance of the corolla like those drawn in Figs. 10-11; in this way they occupy the best possible position just above the stigma, making it easy for the latter to receive the flower's own pollen. Anthers of such species generally lack horns, which are not required to lead the flow of pollen across the stigma.

It was not examined whether these species are self-sterile.

#### *Erica arborea.*

The flowers of this species resemble those of *Calluna* in that the stamens are situated inside the corolla, while the broad stigma is outside on a long style. The pollen is easily shaken out from the flower and hits the stigma both of the same and of other flowers, in large quantities. Fruits are developed in a local greenhouse. A nectary suggests that in its indigenous areas around the Mediterranean the species may also be entogamous.

#### 4. *Pyrolaceae.*

##### *Monotropa hypopitys.* Fig. 18.

The flower has been described by KNUTH (p. 56), who believes that entomogamy is certain and autogamy impossible. Only once, however, did he see a bumble-bee on the flower. I have never seen insects pollinating

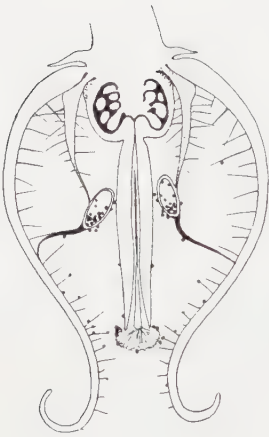


Fig. 16.



Fig. 17.

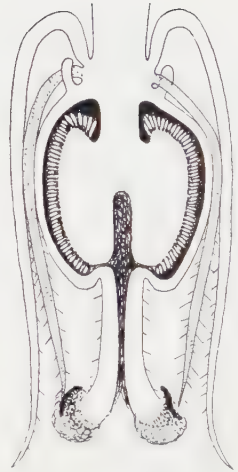


Fig. 18.

Fig. 16. *Andromeda polifolia*. Longitudinal section of flower in autogamy. ( $\times 11$ ).  
 – Fig. 17. *Pyrola media*. Longitudinal section of flower in autogamy. ( $\times 7$ ). –  
 Fig. 18. *Monotropa hypopitys*. Longitudinal section of flower in contact autogamy.  
 ( $\times 7$ ).

the flower in Denmark. Yet, it is fragrant, and a rather long nectary projects into a plainly visible spur at the petals. At our latitudes, however, entomogamy is scarcely of any quantitative significance.

A median microtomic section shows plainly that the flower has contact autogamy, which is rare in any of the other species of *Bicornes*.

The cavity of the flower is narrow, the petals pressing the long stamens tightly against the thick ovary. Through this arrangement the anthers are pressed inwards against the broad stigma, whose large mucilage plug retains a quantity of pollen with the result that the canal of the style is soon densely filled with pollen tubes. This autogamy is very precise in its operation.

#### *Pyrola minor.*

This flower has been described by WARMING, KNUTH and others. They all agree that insect visits are very rare; but yet, almost all flowers develop fruits even in Greenland. Even if insects are kept out by covering up the flowers in bags, many fruits will nevertheless develop and insects are consequently not necessary for the fertilization and play no quantitative role. The fact that hybrids may be formed with other species (*P. rotundi-*



*folia*) shows that fertilization by foreign species is quite possible, but the pollen may also easily be carried by the wind.

The petals are not accrete, but they sit so closely together that the pollen is not easily wasted by being blown away between the petals. Flowers which have been bound up in bags are completely powdered by pollen all over the inside; the stigma is also filled with the flower's own pollen which has sent numerous pollen tubes down through the canal of the style.

#### *Pyrola media*. Fig. 17.

As the opening of the corolla is a little larger and the style slightly longer than in *P. minor*, the chance of anemogamy is correspondingly greater. The species is believed to have come into existence as a hybrid between *P. minor* and *P. rotundifolia*. The corolla of the latter is quite open so that the wind will take away most of its pollen of which very little hits the stigma. If flowers of *P. rotundifolia* are placed under a glass dome no pollen is disengaged.

Like most of our other *Bicornes* the *Pyrola* species are probably also fertilized most frequently by the flower's own falling pollen. Anemogamy and entomogamy are much rarer and without quantitative significance.

### 5. Generalization.

Only further investigations can establish whether drooping flowers of *Bicornes* from other regions are normally autogamous. As a random sample *Pernettya macrostigma* COL. from New Zealand was examined; its stamens were found to have the same structure as most of the other *Ericaceæ*, bearing plenty of fruit without insect visits.

Since the horns of the anthers which, as shown above, are characteristic of most of the drooping *Bicornes* flowers represent a morphological feature, most of the flowers dealt with in this article are generally "wind-autogamous".

### 6. Summary.

1. Drooping *Bicornes* flowers can be pollinated in various ways and are not specially adapted for entomogamy. On the contrary: they are adapted for autogamy which is by far the most important method of fertilization.
2. The horns of the anthers are not particularly responsive to shocks, because already in the bud they are forced tightly (like steel springs) against the corolla,

the anthers being pressed together into a tube (often coalescing) round the style (Fig. 14) just above the stigma.

3. Very little pollen leaves the fine pores of the anthers at a time and only when the flower is shaken by the wind. The light pollen pours slowly in a very thin stream down through the cavity of the corolla (where no wind can reach it) to the narrow opening of the corolla near the stigma, i. e. anemo-autogamy.
4. The flowers are not self-sterile, bearing plenty of fruit without insect visits, e. g. in arctic regions.
5. Some species have bud-autogamy (Figs. 9, 12), e. g. *Erica cinerea*, *Phyllodoce*, *Cassiope tetragona* and *Arctostaphylos alpina*.
6. A remarkable and common form of autogamy is shown in Figs. 5, 6, 8: When the anthers fall down together with the shed corolla they smear pollen on the stigma.
7. Contact autogamy is found for instance in *Monotropa* (Fig. 18).
8. Thrips-autogamy is normal in *Calluna*, *Erica tetralix*, and perhaps *Phyllodoce* and others.
9. Many species are more or less anemogamous, e. g. *Erica (carnea)* and others, *Calluna*, etc. (Figs. 10, 11).
10. Almost all the species can receive visits of insects, but they have generally pollinated themselves before such visits. Entomogamy is merely accidental and not indispensable.

### Literature.

- BEIJERINCK, W., 1940: *Calluna*. Verh. d. Kon. Nederl. Akademie van Wetenschappen, Afd. Natuurkunde. II Sectie, Deel XXXVIII, No. 4, p. 1-180.
- COWAN, J. M., 1950: The *Rhododendron* Leaf. P. 1-116. London.
- DRUDE, O., 1889: Ericaceae. Engler und Prantl: Natürl. Pflanzenfam. Teil IV<sub>1</sub>, S. 1-80.
- HAGERUP, O., 1950: Thrips Pollination in *Calluna*. Kgl. Danske Vidensk. Selskab Biol. Medd. Bd. 18. No. 4. p. 1-16.
- 1951: Pollination in the Faroes in spite of rain and poverty in insects. Kgl. Danske Vidensk. Selskab Biol. Medd. 18, No. 15, p. 1-48.
- HAGERUP, E. and O., 1953: Thrips Pollination in *Erica tetralix*. New Phytologist. Vol. 52, p. 1-7.
- HÖEG, O. A., 1925: Blomsterbestøvningen på Spitsbergen. Naturen. S. 202-220. Bergen.
- KNUTH, P., 1898-99: Handbuch der Blütenbiologie. Bd. II, 2. S. 28-56. Leipzig.
- NORDHAGEN, R., 1937-38: Studien über die monotypische Gattung *Calluna* Salisb. Bergens Museums Årbok. Naturvidensk. Rekke, No. 4, 1. S. 1-42 und 1-70.
- WARMING, E., 1908: Ericaceae. Arctic Flowering Plants. I, p. 1-71, and Medd. over Grøn. Bd. 36.

## Om *Polyporus caesius* og *Ditiola radicata* som Tømmersvampe

Af L. HARMSSEN

Foranlediget af en omfattende undersøgelse<sup>1)</sup> af skader på bygnings-tømmer forårsaget ved angreb af Poresvampe, hvis overflademycel og mere eller mindre vel udviklede frugtlegemer forbliver hvide, har det været nødvendigt at inddrage forekomster i naturen af lignende karakter i undersøgelsen. Arbejdet med *Polyporus caesius* må betragtes som et led i disse undersøgelser. *Ditiola* er ikke nogen Poresvamp, men med sit hvide mycel og dybtgående ødelæggelse også af gavntræ følger den sig naturligt ind i dette arbejde.

### *Polyporus caesius* (SCHRAD.) FR.

Blandt de mange Poresvampe, som man finder på faldne træer og grene i skoven, er der flere hvide. Disse hvide, mere eller mindre konsolformede arter kan være vanskelige at bestemme, men een af de lettest kendelige er *Polyporus caesius*, blålig Poresvamp, der – som navnet antyder – oftest har et blåligt skær. Undertiden kommer den bla farve først frem ved tryk eller beskadigelse af frugtlegemet.

Frugtlegemets form kan være ret varierende, hyppigst konsolformet med ret snæver basis og skarp rand med porer helt ud til randen. Overfladen er håret til filtet, hvid til grå eller gråblå. Som regel forekommer de enkeltvis, men ses også taglagte med meget bred tilhæftningsflade og porelaget undertiden nedløbende på substratet eller helt resupinate. På undersiden af henliggende brædder og lignende kan frugtlegemet ofte være næsten kreds rundt og fæstet til træet ved en midtstillet tynd stilk fra

<sup>1)</sup> Til undersøgelsen har forfatteren modtaget en meget betydelig støtte fra „Statens almindelige Videnskabsfond”, hvorfor jeg er fondet megen tak skyldig.



Fig. 1. *P. caesius* (nr. 2911), sporer og basidier. ( $\times 1250$ ). (Spores and basidia.)

oversiden. Kødet er blødt, fibret, i tør tilstand ret hårdt og skørt, hvidt og ofte med blålige strøg. Porelaget er ret tykt, hvidt til gråblåt ligesom poremundingerne, der er fine, uregelmæssige, ofte bugtede, med tynd, finttandet rand. Basidierne er smalt kølleformede,  $3-5\mu$  tykke; sporer aflangt cylindriske, let krummede og oftest med 2 dråber,  $3-5 \times 1-1,5\mu$ , farveløse, i tykke lag blålige (fig. 1). Hyferne i frugtlegemets væv er farveløse, ret sparsomt grenede, flertallet med mere eller mindre stærkt fortykkede vægge,  $4-6\mu$ , og en del finere, tyndvæggede hyfer  $2-4\mu$ , begge med talrige øskendannelser (fig. 2).

Svampen forekommer både på løvtræ og nåltræ, som ligger meget fugtigt. Om forekomster på gavntræ er oplysningerne i litteraturen meget sparsomme, men hos LINDAU-ULBRICH (1928) angives dog, at den også findes på bygningstømmer. Forfatteren har flere gange iagttaget den på forarbejdet træ, dog mest kasserede brædder og stolper m. m. I Sverige er den set på opskyllet flådningsstømmer, hvor den sammen med *Ditiola radicata* har forvoldt dybtgående skade. I Danmark er den fornylig påvist på bygningstømmer i en gård; her fandtes en række frugtlegemer på en bjælke under gulvet til et loftsrums, hvor taget var utæt.

Det angrebne træ bliver brunfarvet og falder hen i små sprækkeklodser, længdesprækningen er mere udpræget end tværsprækningen. Et overflademycelium er kun svagt udviklet og mangler oftest. Ødelæggelsen kan betegnes som brunmuld og i overensstemmelse hermed giver renkulturer negativ reaktion med oxidaseprøver, både med gallussyre og tannin som med rødkålekstrakt (JØRGENSEN & VEJLBY, 1953).

Renkulturer kan let fås fra frugtlegemets væv og fra det angrebne træ, derimod er det hidtil ikke lykkedes at få sporer til at spire på kunstigt substrat. Myceliet på maltagar er hvidt, tyndt og uregelmæssigt, med mere eller mindre tydeligt radiært strakte partier, hvor myceliet er helt gennemsigtigt og blankt, ligesom fugtigt. Tillige iagttages en ret stærk skrumpning af substratet under myceliet. Hyferne er ret tyndvæggede, i luftmyceliet (fig. 3) ofte uregelmæssige, undertiden opsvulmede, og i

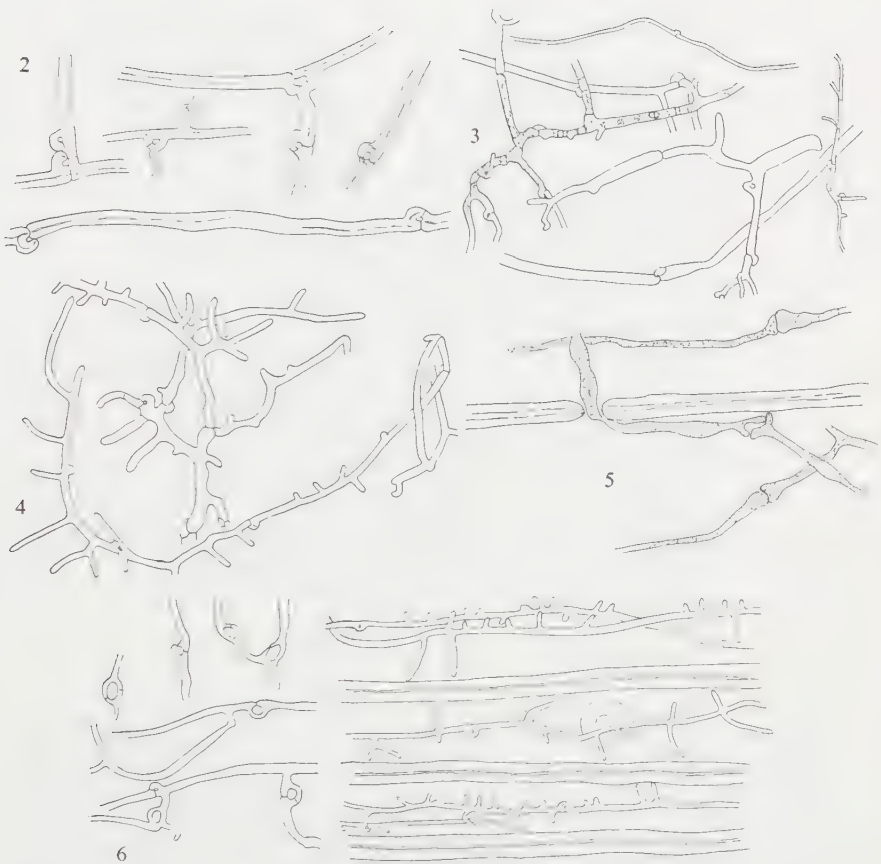


Fig. 2. *P. caesius* (nr. 2911), Hyfer fra frugtlegete. ( $\times 400$ ). (Hyphae from fruit body.) – Fig. 3. *P. caesius* (nr. 2911), Hyfer fra luftmycelium. ( $\times 400$ ). (Hyphae from aerial mycelium.) – Fig. 4. *P. caesius* (nr. 2679), Hyfer fra substratmycelium. ( $\times 400$ ). (Hyphae from submerged mycelium.) – Fig. 5. *P. caesius* (nr. 3427), Hyfer i borehul i trakeidevæg, originale materiale, gran. ( $\times 1000$ ). (Hyphae in bore-hole in tracheid wall, Norway spruce.) – Fig. 6. *P. caesius* (nr. 3427), Hyfer i gran, renkultur, 2 mdr. ( $\times 400$ ). (Hyphae in wood (Norway spruce), pure culture, 2 months old.)

substratmyceliet (fig. 4) især karakteriseret ved langstrakte hyfer med talrige, næsten vinkelret udstående, korte sidegrene. Overalt findes talrige øskendannelser, tildels udformet som medaillonøskner. I ved af gran og fyr angrebet af renkulturer genfindes de samme langstrakte hyfer med korte sidegrene, de synes dog kun at være til stede ved unge angreb (fig. 6). Tillige ses sparsomt grenede hyfer med medaillonøskner. Hyferne passerer trakeidevæggene gennem ret store huller (fig. 5).





Fig. 7. *Ditiola radicata* (nr. 2776), Frugtlegemer på træ.  
( $\times 1.7$ ). (Fruit bodies on wood).



Fig. 8. *Ditiola radicata* (nr. 2776), Hyfer fra luftmycel. ( $\times 200$ ). (Hyphae from  
aerial mycelium.)



Fig. 9. *Ditiola radicata* (nr. 2776),  
Hyfer fra luftmycel. ( $\times 500$ ). (Hyphae  
from aerial mycelium.)

Svampens betydning som bygningssvamp må anses for at være ret ringe. Dels kræver den en så stor og stadig fugtighed, som kun undtagelsesvis er til stede i en bygning, dels synes dens nedbrydning af træet at foregå ret langsomt at domme efter nogle endnu ikke afsluttede forsøg. I et 4-måneders forsøg er konstateret et væggtab på 15–22% for gran og 11–13% for fyr. I naturen forekommer den hyppigst på træ, som er eller har været angrebet af andre svampe.

#### *Ditiola radicata* (A. & S.) Fr.

I modsætning til *Polyporus caesius* forekommer *Ditiola radicata* på træ, som er frit udsat for solens og vejrets påvirkning og derfor periodisk er helt tørt. Den ses som hvidlige til orangegule, millimeterbrede, skiveformede hoveder på en kort, tyk stok, 4–5 mm høj, undertiden 2- eller 3-delt (fig. 7). Ofte fremkommer de rækkevis langs revner i træet. Her i landet og i Norge og Sverige, hvor forfatteren har haft lejlighed til at iagttage den, synes den at være en vel afgrænset art. Så ansete forskere som BOURDOT og GALZIN vil dog ikke anerkende den som selvstændig art, langt mindre som hørende til en særlig slægt, men henfører den til en underart – *stipitatus* af *Dacryomyces deliquescens* BULL., idet de hævder, at der findes alle overgangsformer mellem *Ditiola radicata* og *stipitatus*. NEUHOFF (1936), som bl. a. har skrevet en monografi over Sveriges bævresvampe, opretholder dog arten.

På overfladen af det angrebne træ ses intet mycel, men splitter man det op, ses det, at stokken har en rodliggende forlængelse ind i veddet – deraf navnet *radicata*. Nær overfladen vil marvstrålerne ofte ses som lyse striber fyldt med det hvide mycel, og i skruperevnerne kan findes sejge, hvide mycelflager. Træet mørnes, misfarves over gulbrune til mørkere farver, skrumper og sprækker på grund af nedbrydningen.

Svampen angriber nåletræ, både gran og fyr. I skoven kan den findes

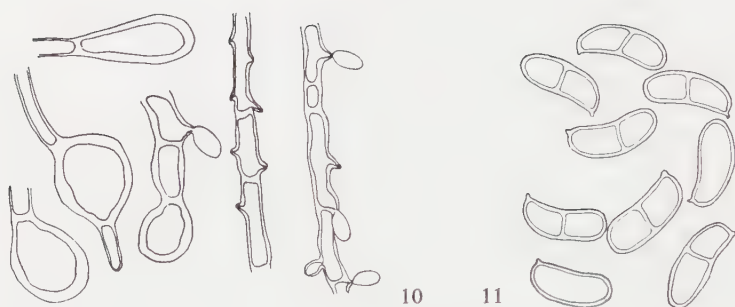


Fig. 10. *Ditiola radicata* (nr. 3031), Klamydosporer, konidier og konidiedannende hyfer fra luftmycel i renkultur. ( $\times 1250$ ). (Chlamydospores, conidia and conidiophores from aerial mycelium in pure culture). – Fig. 11. *Ditiola radicata* (nr. 3259), Basidiesporer. ( $\times 1250$ ). (Basidiospores).

på henliggende, tynde stammer udsat for sol og vejrligets skiften. Ellers på forarbejdet træ i fri luft, f. eks. bænkesæder, hegn og plankeværker. På grundlag af iagttagelser af dens forekomst i en række år synes den at foretrække træ af ret små dimensioner, 1–2 tommers tykkelse, men den kan dog også findes på svært tømmer, idet der i Sverige er iagttaget meget kraftige angreb på flådningstømmer op til 12 tommers tykkelse.

Som bygningssvamp kendes den fra vinduesrammer og karmtræ og tillige fra udvendige døre. Skaden kan blive meget dybtgående, men den breder sig langsomt, og ødelæggelsen går ind under betegnelsen almindelig råd. Iøvrigt kan angrebet sidestilles med angreb af *Lenzites*-arterne – Korkhat – som er meget modstandsdygtige mod udtørring.

Myceliet er opbygget af farveløse, ret sparsomt grenede, tykvæggede hyfer med få tværvægge og uden øskendannelser. Her og der finder man i myceliet ejendommelige, garnnøglelignende dannelser (fig. 8 og 9), som ses særlig tydeligt i mycel fra renkulturer, og man kan her finde alle trin fra nogle få vindinger til mere eller mindre regelmæssigt spiralformet liggende hyfer.

I renkultur vokser svampen meget langsomt, myceliet er hvidt, mat, tæt og sejt med en uregelmæssig overflade. Påfaldende er den stærke skrumpning af substratet lige under myceliet. På luftmyceliet dannes talrige konidier (fig. 12), aflange og ofte let krummede,  $3\text{--}6 \times 2\mu$ , og tykvæggede, farveløse klamydosporer (fig. 10), ovale til kugleformede,  $8\text{--}12 \times 5\text{--}8\mu$ . Basidiesporerne (fig. 11) er farveløse,  $9\text{--}10 \times 4\mu$ , undertiden 2-delte. De spirer let på maltekstraktagar. Prøverne for Oxidase giver usikre reaktioner, fra negativ til svagt positiv, både med gallussyre og tannin som med rødkålseksakt.

## Summary.

*Polyporus caesius* and *Ditiola radicata* as timber fungi.

*Polyporus caesius* (SCHRAD.) FR. occurs in nature on both hardwood and softwood. The cracking of the attacked wood is like that caused by attack of *Coniophora cerebella*. Pure cultures give no reaction to oxidase tests, neither gallic and tannic acid nor red cabbage extract (JØRGENSEN & VEJLBY, 1953).

Pure cultures are easily made from the flesh of fruit bodies or from attacked wood, but germination of the basidiospores has failed. The mycelium is white, thin and irregular; it has more or less distinct, radially extended parts where it is transparent and glossy. The substrate shrinks rather much below the central part of the mycelium. The hyphae are thinwalled with numerous clamp connections, partly as "medallions". The submerged mycelium is characterized by long hyphae with numerous short branches at right angles (also found in wood attacked in pure cultures at least in young stages) besides little branched hyphae with "medallions". It has been found once on a joist.

*Ditiola radicata* (A. & S.) FR. is most often found on worked softwood but it also occurs in nature on logs exposed to sun and weather. It is seen as small, 1–2 mm. broad heads on 4–5 mm. high, thick stalks, whitish to orange yellow. White, tough mycelium sheets are found in the cracks. The fungus causes decay on window frames, outward doors, benches, fences etc. and seems to prefer wood of fairly small dimensions, 1–2 inches across, though it is also found on heavy logs. The decay is like that caused by *Lenzites saepiaria*.

The growth in pure culture is very slow, the mycelium is white, dense and tough with an irregular surface. The shrinking of the substrate below the mycelium is conspicuous. The hyphae are colourless, thickwalled, fairly little branched, with few septa and no clamp connections. In the aerial mycelium peculiar formations are seen like balls of yarn, consisting of spirally winding hyphae. Numerous conidia are formed,  $3-6 \times 2 \mu$ , and thickwalled chlamydospores,  $8-12 \times 5-8 \mu$ . The oxidase tests give weak and doubtful reactions.

## Litteratur.

- BOURDOT, H. & GALZIN, A., 1928: Hyménomycètes de France.  
 CARTWRIGHT, K. ST. G. & FINDLAY, W. P. K., 1946: Decay of timber and its prevention.  
 CUNNINGHAM, G. H., 1948: New Zealand Polyporaceae, 3. The genus *Polyporus*. Bull. Dep. Sci. Industr. Res. N. Z. no. 74.  
 JØRGENSEN, E. & VEJLBY, K., 1953: A new polyphenol oxidase test. *Physiologia Plantarum*, 6.  
 LINDAU-ULBRICH, 1928: Kryptogamenflora, Bd. I. Die höheren Pilze. 3. Aufl.  
 LOWE, J. L., 1942: The Polyporaceae of New York State (Except *Poria*). Bull. N. Y. St. College Forestry. Techn. Publ. no. 60.  
 NEUHOFF, W., 1936: Die Gallertpilze Schwedens. *Arkiv f. Botanik*, 28 A.  
 NOBLES, M. K., 1948: Identification of cultures of wood-rotting fungi. *Canad. Journ. Research*, C. 25.

## A New *Oxytropis* Species from Alaska

By ERIC HULTÉN

The genus *Oxytropis* is concentrated in central Asia. Fl. SSSR enumerates 276 species, most of which grow in Tian Shan and Pamir.

Northward the number of species diminishes rapidly, only 23 being at home in northeastern Asia, 9 of which belong to the flora of Kamtchatka. Scandinavia is reached by 4 species only. The American *Oxytropis* flora is comparatively poor, about 19 species being known from Alaska-Yukon and only 8 from eastern America, while the genus is lacking in the Greenland flora. In Alaska several endemic species with a comparatively small area of distribution occur.

In a collection made by Professor A. R. HODGDON in 1952 in the vicinity of the upper Kurupa R., (a tributary to Colville R. on the Arctic slope of Alaska, approximately 67° 30' N. lat. and 155° W. long.) kindly sent to me for examination, included a very characteristic *Oxytropis* species, differing from all other species of that genus known to me in being completely glabrous. Although only a single collection has been seen I do not hesitate to describe it as a new species.

### *Oxytropis glaberrima* n. sp.

*Planta tota glaberrima, caespitosa.*

*Caules lignescens et caudice robusto subterraneo exeuntes, iteratim ramosi, residuis stipulorum et petiolorum e compluribus annis obtecti. Folia 1–2 cm. longa. Pars connata stipulorum alba; pars libera lanceolata vel deltoidea acuta viridis, margine glabra vel glandulis parsissime obsita. Pinnae 7–11 involutae, lanceolatae, 3–4 mm. longae, 1 mm. latae, acutae, uninerviae. Pedunculi biflori, 2–3 cm. longi. Bracteae circiter 3 mm. longae, lineares. Calyx turbinatus violaceus, dentibus anguste deltoideis, 3–3.5 mm. longis. Petala coerulea; vexillum alas et carinam superans. Legumen juvenile sessile, glabrum, rostro abrupte hamato; legumen maturum ignotum.*





Fig. 1. *Oxytropis glaberrima* HULT. n. sp. About  $\frac{3}{4}$  natural size.

Alaska: Upper Kurupa River valley elev. about 3000 ft., 7 miles N.W. of Kurupa Lake June 25, 1952 A. R. HODGDON 8066. Type specimen (Fig. 1) in Riksmuseum, Stockholm.

This plant is characterized by being completely glabrous and by its violet-coloured calyx. It somewhat resembles *O. revoluta* LEDEB. from Kamtchatka, which, however, has a stipitated pod and *O. Hudde!sonii* PORS. from the vicinity of Whitehorse in Yukon, but differs *inter alia* in the above-mentioned characteristics. It is probably closer related to the latter species.

# Universitetets botaniske haver

## Historie, formål og tilstand

Af H. NILAUS JENSEN

I tilslutning til studiet af planterne, såvel deres systematiske som deres biologiske og fysiologiske forhold vil det altid være en uvurderlig hjælp at kunne dyrke dem og studere deres livsforhold på levende materiale, og det var vel dette behov, der affødte begrebet Botaniske haver.

Medens de første botaniske haver i Europa daterer sig fra den sidste halvdel af det 16-ende århundrede, finder vi den første og ganske spæde begyndelse til en botanisk have ved Københavns Universitet dateret til året 1600.

Begyndelsen formede sig således, at der i det nævnte år skulle bygges en "Residenz" d.v.s. en bolig for en af Universitetets professorer omtrent på det sted, hvor Zoologisk Musæum nu ligger ud til Krystalgade (det daværende Skidenstræde), og det blev da samtidig besluttet, at et jordareal „220 Fødder i længden og 110 Fødder i bredden" skulle udlægges til en medicinsk-botanisk have. I et „Kongeligt Skiøde og Gave-Brev" af anden august 1600 læser vi „Og efterdi fornævnte Plads udi så lang Tiid haver lagt øde og ikke derpå er fået nogen Bygning; Så og efterdi Universitetet der udi fornævnte vor Kiøbstad Kiøbenhavn er med en ny Residentz blevet forbedret; Thi have vi nådigst undt, skiødt og givet, og nu med dette vort åbne brev unde, skiøde og give formeldte Plads til Universitetet der sammesteds så det altid herefter skal ligge og bruges til en Have til formeldte Residence, hvorudi kan ympes og plantis synderlige Simplicia, og skal den Professor, som i formeldte Residentze bliver boendes, dermed have Opseende." Der blev dog ikke samtidig bevilget nogen midler til at holde haven for og heller ikke ansat nogen til at passe haven, som snart betegnes Hortus botanicus og snart Hortus medicus, så dens vedligeholdelse var afhængig af, hvem der beboede boligen. Professor Rottbøll skriver således „thi da man af førstningen

formodentlig allene har tænkt deri at indtage vore vilde planter, har man troet, at dertil ingen udgifter behøvedes og derfor ey heller tillagt den indkomster". Botanikken var på dette tidspunkt nærmest en disciplin, der var underordnet medicinen, og det vigtigste mål for det botaniske kendskab til planterne var derfor deres medicinske anvendelse. Desværre var det ikke altid den medicinske professor, der havde den pågældende bolig, og imellem har vel havens opgave nærmest været at tjene som lysthave.

Af bekendte mænd vides det, at såvel OLE WORM som RASMUS CASPER BARTHOLIN har benyttet haven. Sidstnævnte skænkede i 1696 et legat på 1200 „Kronedalere", „Hvoraf dend årlig Rente skal bruges til hielp at holde en Urte Gaards-Mand for in Horto Botanico, samt at kiøbe fremmet Frøe og Planter". I 1723 klager JOHANNES DE BUCHWALD over denne dobbelte brug af haven dels som lysthave og dels som botanisk have og ønsker den delt til hver sit brug. BUCHWALD udgav i 1720 en på latin skrevet bog „Specimen Medico-Practico-Botanicum" med beskrivelse af en del urters anvendelse. Denne bog blev i 1721 af hans søn BALTHASAR JOHANNES DE BUCHWALD oversat til tysk og af denne fremgår, at planterne i haven i 1719 er blevet omplantede og anbragt i alfabetisk orden. Havens areal blev efter ildebranden i 1728 yderligere formindsket, men først efter 1769 hvor CHRISTIAN VII ved kgl. reskript af 3. februar skænker Universitetet 2500 dalere, hvoraf renten skulle gå til havens „istandsættelse og bestandige dyrkelse", lysner det lidt; tillige lover kongen, at Communitetets Have, samt de haver, som sognepræsten og 1-ste kapellanen ved Frue Kirke benyttede, skulle blive lagt til haven, når de pågældende embeder blev vakante. Disse forbedringer blev dog aldrig gennemførte, men den medicinske professor CHRISTEN FRIES ROTTBØLL var glad for planen og havde i denne periode fået bygget det første drivhus, der var 16 fod langt og 8 fod bredt og lå ud mod Skidenstræde; han udtaler følgende om haven „jeg kan calculo mathematico bevise, at der med al magelighed kan stå over 2000 species, som er alt, hvad den upsalske have har". Universitetet modtager fra kongen et tilbud om at få en del af OEDERS botaniske have, der lå ved Amalienborg sammen med et der beliggende Bibliotek samt 5000 rdl. til istandsættelse og 300 rdl. til vedligeholdelsen.

I 1770 flyttedes så den Botaniske Have under professor ROTTBØLL's ledelse ind til en i drift værende have, der på foranledning af FREDERIK V var anlagt af bayeren GEORG CHRISTIAN OEDER, der var indkaldt til landet af J. H. E. BERNSTORFF i årene omkring 1752. Denne såkaldte OEDER's have blev ved anlæggelsen af Amaliegade delt i to dele, hvoraf den mindre

vestlige del, der var lidt over 11000 kvadratalen og havde flere væksthuse, blev overladt Universitetet, medens den ca. dobbelt så store, østlige del blev tilknyttet det nyanlagte Frederiks Hospital og lededes af OEDER, der af kongen udnævntes til Medicus. Det var udfra denne stilling, at OEDER begyndte udgivelsen af *Flora Danica* i året 1761.

Som gartner ved den botaniske have ansattes hollænderen J. W. KÆSEMACHER med en løn af 200 rdl. samt 60 rdl. til husleje og brændsel.

Det blev dog kun en kortvarig glæde. Universitetet fik af denne have, idet Kommercekollegiet allerede i 1777 fik brug for arealet, og Kongen tilbagekøbte haven for en sum af 6000 rdl. og skænkede Universitetet grunden til en ny have ved Charlottenborg, og allerede året efter flyttedes inventar og planter dertil. Det faldt altså endnu en gang i professor ROTTBOLL's lod at være med til at flytte haven til et nyt sted. Samtidig ser man, at nu er botanikken ved at udvikles til en selvstændig videnskab, idet MARTIN VAHL i 1779 blev lektor i botanik, og derved indledte en ny æra for det botaniske studium. Denne nyordning medførte i årene omkring 1787 nogle stridigheder angående lektorens ret til at benytte havens materiale og medførte, at VAHL søgte sin afsked fra stillingen. Han fik dog senere oprejsning ved at blive udnævnt til professor, men først efter at ERIK NISSEN VIBORG havde været professor i botanik fra 1797 til 1801, hvor han blev kaldet til at lede den nyoprettede Veterinærskole, og MARTIN VAHL ansattes i hans sted.

Da Universitetet ikke alene rådede for haven, men Kongen også havde ejendomsret til den og af og til ydede tilskud, var dens ledelse lagt i hænderne på to direktører, nemlig professor ROTTBOLL valgt af Universitetet og geheimeråd T. HOLMSKJOLD valgt af Kongen. I 1798 udvidedes direktionen til at bestå af statsminister C. F. REVENTLOW og professorerne WOLDIKE, VAHL og VIBORG. I 1817 gik haven helt over til Universitetet, og professor JENS WILKEN HORNEMANN blev enedirektor. HORNEMANN var blevet professor efter VAHL's død i 1804. Efter hans død i 1841 tiltrådte JOACHIM FREDERIK SCHOUW, som trak sig tilbage i 1852 og afløstes af FREDERIK MICHAEL LIEBMANN.

LIEBMANN havde fra 1845 været ekstraordinær professor, efter at han i årene 1840–1843 havde været på studierejse i Mexiko og derfra havde hjembragt store samlinger til det botaniske herbarium og tillige en del levende planter til haven, bl. a. den endnu levende store *Dioon edule*. Efter LIEBMANN's død i 1856 blev JOHAN LANGE direktør for haven og den sidste i denne have, idet det blev ham, der efter at have udført et stort forarbejde, var meget virksom for at få haven flyttet til større forhold.

Selve haven ved Charlottenborg var ved anlæggelsen kun på ca. 3 tdr. land, og der blev derfor hurtigt knapt med plads, så der måtte ryddes op i bestanden af træer, ligesom gangene måtte gøres smallere, og en del Buksbombhække fjernes. I 1803 skænkede Kongen 3000 rdl. til et væksthushus, der var  $71\frac{1}{2}$  fod langt, 14 fod bredt og  $10\frac{1}{2}$  fod højt. I 1811 måtte haven afgive et mindre areal til Den kgl. Mont, men til gengæld skænkede Kongen en op til haven stodende grund på 2000 kvadratalen, samt 5000 rdl. til arealets bearbejdning og indhegning. Her skulle indrettes en dam for ferskvandsplanter, en kanal med rindende vand, plantes pil og et anlæg for alpeplanter. I 1843 blev bevilget 9000 rdl. til opførelse af et palmehus 26 alen langt, 12 alen højt og  $11\frac{1}{2}$  alen bredt, og samtidig blev de ældre huse delvis ombyggede. I 1844 fik haven en udvidelse på 6 skæpper land.

Med de her nævnte små udvidelser var havens muligheder dog begrænsede, og det stod klart, at man måtte skaffe et bedre sted til en ny have. Det første forsøg skete allerede i 1803, hvor gehejmeråd CLASSEN tilbød et areal på 8 tdr. land på Osterbro, men af frygt for de udgifter, nybyggerne ville andrage, turde man ikke tage mod dette tilbud. Det andet var ca. 1823, da man forsøgte at få haven slået sammen med den botaniske have ved Rosenborg. Her havde CHRISTIAN IV c. 1633 gjort en begyndelse til en botanisk have ved at lade dyrke et bed med *Simplicia* (lægeurter), dette udvikledes yderligere, da CORFITS ULFELDT i året 1638 havde fået knyttet lægen og botanikeren OTTO SPERLING til haven som dens leder, og hvor der i hans tid var en plantesamling, der langt overgik universitetets have.

Sammenlægningen blev dog ikke til noget, og i stedet blev det efter mange svære fødselsveer muligt at få oprettet en ny have på et areal beliggende på glaciets af det da nylig nedlagte fæstningsterræn, og denne – den nuværende have – stod færdig til at indvies den 9. oktober 1874. Haven ved Charlottenborg blev overladt dels til Kunstakademiet, dels til bebyggelse.

Af de botaniske gartnere, der var virksomme i haven ved Charlottenborg, må nævnes tre, hvis virke foruden i deres embede tillige satte sig spor i det praktiske gartneri, således at de med føje nævnes som fremragende gartnere. I deres gerning i haven var de med til at forme en linje, som endnu delvis følges i havens arbejdsystem, hvorefter noget kan føres tilbage til 1795.

I 1793 udnævntes FREDERIK LUDVIG HOLBOLL til botanisk gartner og dermed indledtes et udmærket samarbejde og inderligt venskab med professor HORNEMANN gennem mange år til gavn for udviklingen af



haven såvel som for botanikken. HOLLBÖLL døde i 1829 og blev afløst af OTTO JOSIAS NIKOLAJ MORCH, der virkede der til sin død i 1842. Efter ham ansattes AUGUST WEILBACH, der efterlod sig et eftermæle som en meget nidkær og duelig embedsmand, og som i arbejdet for havens flytning nedlagde et meget stort arbejde i den kommission, der var blevet nedsat i 1860; han døde i 1868 og nåede således ikke at se planerne fortud i livet. Efter hans død ansattes TH. FRIEDERICHSEN som sammen med havens direktør professor JOHAN LANGE kom til at forestå arbejdet med flytningen.

Om plantebestanden i Charlottenborghaven kan henvises til O. J. N. MORCH: *Katalogus plantarum horti botanici Hafniensis* 1839 og til professor J. F. SCHOUW: Forelobig fortegnelse over den københavnske botaniske haves planter i årene 1842–1846, København 1847. Denne sidste bog er den udførligste og indeholder tillige en plan over haven.

Vedrørende den nuværende haves historie og tilblivelse kan der henvises til C. H. OSTENFELD: Botanisk Have gennem 50 år 1874–1924. København 1924. Her er skildret havens første halvt hundrede år, men da der nu er forløbet yderligere 30 år, vil der måske være et eller andet at knytte hertil.

Forst bør dog nævnes rækkefølgen af de mænd, der som havens ledere har haft æren og ansvaret gennem de 80 år, den har bestået. Professor JOHAN LANGE, der var virksom for havens flytning og især for dens arboretmæssige virksomhed og med fremskaffelse og bestemmelse af havens træer, var dens leder indtil 1876 og afløstes af F. DIDRICHSEN, der var direktør til 1885. Derefter kom EUGEN WARMING fra 1885–1911. C. RAUNKJÆR fra 1912–1923. C. HANSEN OSTENFELD fra 1923–1931, hvor han afløstes af havens nuværende direktør professor KNUD JESSEN, der således har haft en lang virkeperiode i haven.

Medens der har været en række af direktører, har der i den samme periode kun været tre botaniske gartnere. Den første var TH. FRIEDERICHSEN, der tiltrådte i haven ved Charlottenborg i 1868 og fortsatte i den nye have til 1902, hvor han trak sig tilbage og afløstes af AXEL LANGE, der var ansat indtil sin død i 1941. Begge disse mænd var i høj grad med til at præge haven og bringe den frem både hvad udseende og anseelse angår, ikke mindst i international henseende.

I de senest forløbne 30 år er der gerne hvert år foretaget forskellige ændringer i havens anlæg. Den vigtigste var den i 1929 foretagne, hvor hele partiet foran væksthuse blev omlagt i en mere regelbunden stil og derved skabte en bedre harmoni mellem væksthuse og haven, ligesom det noget ørkenagtige præg med de store uregelmæssige gruspladser

erstattedes med plæner og blomsterbede. Nærmere herom kan findes i Beretning om Botanisk Haves virksomhed i årene 1929–1933.

Selve havens drift var selvfølgelig i de fem krigsår 1940–45 udsat for adskillig belastning, og det var med megen ængstelse, man særlig så vintrene imøde, om det ville blive muligt at komme igennem med havens værdifulde plantesamling, det var jo ofte ganske elendigt brændsel, der måtte fyres med, og der kunne jo ske så meget. Noget hjalp det måske, at haven i 1941 fik omlagt sin fyring og fik indlagt helt nye stokerkedler, der næsten kunne tage alt slags brændsel. De bange anelser blev dog ikke til virkelighed, og haven kom godt igennem de svære år kun med et tab på relativt få planter, hvad dog især skyldtes de usædvanlig kolde vintre 1940–43. Medens det kun gik småt frem i de første år efter krigens ophør, bedredes dog forholdene, og haven har siden da forøget sin plantebestand stærkt, nemlig med godt 3000 arter og varieteter, det vil sige med c. 20%, og der dyrkes nu c. 15.500 forskellige former. Det er da også nu således, at man er ved at nå højdepunktet for havens ydeevne, ikke mindst gælder det for væksthushenes vedkommende, således at man må mindske med at optage nye planter til kultur.

På friland har man måttet rydde en del dubletter af træer for at give plads for andre arter.

Med hensyn til havens kapacitet som arboret har det længe været klart, at haven er for lille og kunne bruge meget mere plads, men da Statsarboretet i Horsholm mere og mere kan overtage det arboretmæssige arbejde og ansvar, behøver haven ikke at føle sig så bundet til at bevare de større træer, som tager en uforholdsmæssig plads. Dette står da også som baggrund for en stærkere rydning af træer i haven til fordel for en udvidet plantning af buske, specielt de sjældnere og mere vanskelige former, alt såvidt ikke havens parkmæssige udseende forringes derved.

En af havens opgaver er også at virke som park, således at den kan betjene det publikum, der søger haven for rekreation og ikke for studium. Herved fremkommer der dog ofte visse vanskeligheder, idet man må fremhæve, at dens første formål er at tjene det botaniske studium, og at den som studieplads må hævde sin særstilling. Dette sker da ved skærpede regler for besøg i haven, f. eks. ingen barnevogne og legende børn, eller børn uden voksne ledsagere, ingen legevogne eller cykler, ingen blomster ind og ud af lågerne o. s. v. Haven har da også et stærkere opsyn, idet der altid er placeret en betjent ved hver låge tillige med en patruljerende opsynsbetjent i haven. At haven derved opnår at få et stilfærdigere publikum og en fredelig atmosfære tjener ikke blot de studerende til

gavn, men er også en fordel for det publikum, der gerne vil nyde de smukke omgivelser i fred og ro.

Om havens plantebestand og det botaniske system, hvorefter planterne placeres og bogføres kan nævnes følgende. Medens man i haven ved Charlottenborg først brugte det Linnéiske system, der var nyt dengang, haven anlagdes, og det egentlige botaniske studium tog sin begyndelse, ændredes systemet i 1860 efter ENDLICHER's *Genera Plantarum*, der var trykt i 1836-1840 og opstillede planterne i det såkaldte naturlige plante-system, og hvor planteslægterne opførtes med en slægtsnummerering. Disse af ENDLICHER indførte numre danner endnu stammen i det nummersystem, haven bruger, og hvormed alle de bestemte planter optages og indføres i havens samlinger. Dette system virker så elastisk, at det endnu kan gøre fyldest i det store og hele, selv om der i tidens løb er sket en del ændringer i opfattelsen af planternes indbyrdes slægtskabsforhold. Medens man tidligere indførte planterne i en hovedbog, der så måtte omskrives med nogle års mellemrum, gik man i 1942 over til at benytte kartoteksordningen, hvorved oversigten og tilføjelsen af ny tilkomne arter lettes.

Havens nuværende kartotek rummer ialt c. 20.000 kort, idet princippet er således, at et nummer, der engang er belagt, ikke udskydes eller belægges igen, selv om planten viser sig at være synonym med en anden i samlingen optaget plante, det anføres da på kortet og skulle planten igen gå tilbage til det oprindelige navn forefindes kortet. På kartoteks-kortet såvelsom ude i haven betegnes den enkelte art med et nummer, der opføres som en brok, hvor tælleren er slægtens nummer (efter ENDLICHER) og nævneren betegner arten. Arterne nummereres fra 1 og op efter i den rækkefølge, de optages, og eventuelle varieteter får artens nummer med tilføjelse af B-C-D o.s.v. Den samme bogstaveringsmåde bruges også til nye slægter, der ikke står nævnt hos ENDLICHER, idet de nummereres med bogstaver, der føjes til den slægts nummer, der står den nærmest. På kortet opføres derefter plantens navn, autornavn, hjemsted og varighedsbetegnelse: ○,○○,¼, ½, og iøvrigt med et bogstav, således d for frilandsplanter, fr for koldhus, t for tempereret hus og c for varmhusplanter, altså betegnelser for dyrkningsmåden. Som den sidste, men meget vigtige, oplysning anføres på kortet alle de datoer, da planten har været til revision og er blevet bestemt. Ved hjælp af disse data kan man ved at slå op i de protokoller, der føres over alle plantebestemmelser, se hvorfra den pågældende plante er kommet til haven. Ved at se hvornår planten første gang er blevet bestemt, kan man se hvorlænge planten har været dyrket i haven.

De førnævnte bestemmelsesprotokoller findes i en ubrudt række fra året 1841. De repræsenterer et kontrolsystem, som ikke findes i ret mange botaniske haver og har i højeste grad været medvirkende til, at haven her har erhvervet et godt ry ude i verden for korrekt benævnte planter.

Før denne side af havens virke nærmere skal omtales, skal nævnes lidt om havens sakaldte ubestemte planter. Haven har det princip, at enhver plante, der kommer fra en anden have enten som frø eller plante bogføres i havens tilgangsbøger for de sàs eller plantes. Hvis det drejer sig om hjemkommet frø betegnes det, foruden med navnet, overst på etiketten med en brøk, hvor havens navn sættes overst og årstallet under strengen. Haven tager årligt mellem 2–3000 portioner frø hjem. De levende planter, der kommer hjem til haven – i reglen 6–700 årligt – indføres i en særlig bog og etiketteres med en brøk, hvor tælleren er årstallet med et P foran og nævneren er plantens lobenummer. Disse bogforingsmåder kan med en ændring i 1902 føres tilbage til 1795, og alle havens tilgangsbøger er i behold tilbage til dette år. De ovenfor nævnte planter står nu med denne betegnelse, indtil de blomstrer, og når dette sker, sendes de til bestemmelse. Plantebestemmelsen foretages af en botaniker, der betegnes haveamauensis, som har sin arbejdsplads på Botanisk Museum. Her gennemgås planten og sammenlignes med beskrivelse, eventuelle billeder eller herbariemateriale, således at det konstateres, om planten har det rette navn, eller om den skal kaldes noget andet, hvilket ofte kan være tilfældet. Navnet indføres i bestemmelsesprotokollen, der altså er et meget vigtigt led i havens system. På havens kontor udskrives så resultatet på bestemmelsessedler, der efter at være rettede i havens bøger, specielt dens hovedkartotek, går ud til afdelingerne i haven og får etiketterne rettede i overensstemmelse med bestemmelsesresultatet. Der bestemmes fra 1000 til 1200 planter årligt.

Foruden denne den vigtigste kontrolforanstaltning har haven også en anden, men dog ikke så virksom måde, skønt den dog undertiden afslører en og anden fejl. Det drejer sig om havens afkontrollering af det frø, der høstes i haven, det vil sige om c. 4000 slags frø årligt. Almindeligvis høstes der frø af alle de planter i haven, som giver frø. Efter rensningen bringes det op på havens kontor, hvor det kontrolleres ved hjælp af havens store samling af originalfrø. Denne frøsamling fremkommer på den måde, at såsnart en plante har givet frø for første gang, får den en frøpose lavet af dokumentpapir og hvorpå anføres de samme oplysninger som på kartotekskortet; i denne pose fyldes der lidt frø af den nye høst, og samtidig anføres årstallet på posen. Hvergang arten senere giver frø, sammenlignes dette med frøet i posen, og der lægges stadig noget nyt



frø i den, så man eventuelt kan tage af dette til at så på ny, hvis planten mistes. Til de en-årige planter tages der samtidig frø fra til udsæd. Bliver en sådan plante bestemt, anføres dette på posen samt tillige, hvorfra planten i det enkelte tilfælde stammer. Af såvel den første høst som i reglen ved senere bestemmelser fyldes lidt af hosten i en særlig kapsel, og disse repræsenterer det egentlige originalfrø og mærkes med årstallet og et udråbstegn. Ved hver fremtidig høst bliver frøet sammenlignet med frøet i posen, for det bruges til uddeling. Alle oplysninger vedrørende frøet føres på posen, og desuden føres såvel al udsæd som høst i havens store såringskatalog, hvori alle havens bestemte planter er opført.

Dette system med originalfrøet kan føres tilbage til året 1795, og man kan endnu finde enkelte gamle originalposer fra denne tid, selv om de fleste har måttet omskrives i tidens løb. De ældste poser er i reglen lavet af og skrevet på bagsiden af gamle dokumenter altså gennemført med økonomi. Disse poser er ofte i stand til at give gode oplysninger om planternes historie gennem tiderne.

For at man til enhver tid kan vide besked med havens plantebestand – for tiden c. 15.500 – bliver alle planter hvert år afmærkede i særlige specialkataloger. For frilandsplanter med betegnelsen på det sted, planten står, for træerne med antal af individer for hver art, for husplanterne med husets nummer og i reglen også antal af individer. Er der i årets løb arter, der er døde, bliver de sået igen, såfremt der findes spiredygtigt frø. Disse specialkataloger såvelsom det store såringskatalog må omskrives med 5 à 6 års mellemrum og sammen med afmærkning, frøkontrol m. m. repræsenterer det et stort kontorarbejde, der dog er nødvendigt, om haven skal holde sin standard.

Om selve havens arbejde såvel indadtil som udadtil kan der iøvrigt henvises til de 5-årsberetninger haven udsender.

Med sin store arbejderstab, der i sæsonen omfatter nær et halvt hundrede mand, vil det forstås, at haven har et stort budget at arbejde med; foruden selve havens regnskaber føres også fra havens kontor regnskaberne for Botanisk Centralbibliotek, Botanisk Laboratorium, Botanisk Museum og Plantefysiologisk Laboratorium.

Foruden botanisk gartner og den fornævnte haveamanuensis (botaniker) fordeler havens arbejdsstab sig således: 3 afdelingsgartnere, hvoraf 1ste afdelingsgartner leder frilandsafdelingen samt har ansvaret for frøudvekslingen m. m. De to andre afdelingsgartnere leder henholdsvis formeringsafdelingen og væksthushafdelingen. 1 assistent der bl. a. fører regnskaberne, udfører korrespondancen og andet kontorarbejde. Disse fire er havebrugskandidater, og deres ansættelse sker ved Universite-



tets rektor. Endvidere er der af fastansatte 5 formænd, 13 gartnermedhjælpere og 3 opsynsbetjente, 1 varmemester og 2 fyrbødere samt 1 materialsnedker og 1 kontorbetjent.

Dertil kommer af timelønnet personale 11 gartnermedhjælpere, hvoraf 3 har helårsarbejde, 4 gartneriarbejdere samt en rengøringskone. I sommertiden beskæftiges tillige 2 ekstra opsynsbetjente.

## Dating of Sand-drift East of Ulfborg

By H. JONASSEN

One of the biggest areas of inland dunes in Jutland is found east of Ulfborg, West Jutland. It forms a landscape of big hills. On some places drifted sand is seen in dunes with *Elymus arenarius*. Most of the hills are covered with *Calluna* and plantations of spruce and pine as Ulfborg, Straasø, Klovsig and Thorsted plantations.

The river Madum aa is running through the country coming from south-east and in the central part turning towards south-west. At the central part, north of Lystbæk gaarde, the valley is narrow, the drifted sand coming down to the river which has cut its way one meter down through the sand in a narrow channel. East of that place a layer of diatomite is to be seen in the river bank. The following section was measured:

- 0– 35 cm. sand without stones.
- 35– 88 cm. grey, when dry white, diatomite.
- 88– 95 cm. sand with ocher in the lower part.
- 95–100 cm. black humified sand with horizontal branches.
- 100 cm. + grey sand.
- River surface at 115 cm.

East of the section the valley expands. Where it is broadest Filso lake is situated, nearly overgrown by *Phragmites*.

East of diatomite section the bottom of the plane valley has been cultivated in grassfields. Several drillings were made between the river and the foot of the hillside forming the edge of the valley. The diatomite continued about 200 m towards east, resting on mud; the two layers, in all 1 to 1.5 m., rested on sand without stones. The mud contained seeds of *Nuphar luteum* and *Nymphaea alba* as well as fruits of *Potamogeton praelongus*.

Further east the grassfield changed into a rather wet vegetation containing *Menyanthes trifoliata*, *Holcus lanatus*, *Carex panicea*, *Poten-*

*tilla erecta*, *Hydrocotyle vulgaris* and *Amblystegium*. Drillings showed a layer of brown mud with roots of *Carex*, seeds of *Nuphar*, fruits of *Scirpus lacuster* and *Potamogeton praelongus*. Below one of the sections:

- 0– 15 cm. brown fen peat.
- 15– 85 cm. brown mud with fruits of *Scirpus lacuster* and *Potamogeton praelongus*.
- 85– 92 cm. grey sand without stones. Pollen of *Myriophyllum alterniflorum*.
- 92–110 cm. brown crumbling forest peat with branches and bark of birch. The lower centimeters rich in radicels of *Carex*.
- 100 cm. + grey sand.

The above section is one of many measured along a line south-north from the edge of the valley to the south bank of Madum aa. They were all the same except that they were without peat in the bottom. The section showed a quite flat bottom with the forest peat resting in a very shallow basin.

The situation seems to indicate that drifted sand has dammed up Madum aa forming a barrier north of Lystbæk gaarde. In this way Filso has been formed. In a calm bay south-east of the outlet through the barrier the diatomite has been deposited; as the outlet has cut through the barrier the water has been lowered in the lake which has nearly disappeared.

From the top to the bottom the diatomite contains pollen of beech. If the above given supposition as to the formation of the diatomite is right it means that the sand-drift which dammed up Filso took place at one or another time of the beech period. Fig. 1 shows a diagram from the above mentioned section from the fen. It shows that the forest peat is from the pine period and the beginning of the oak period. Birch bark and branches in the peat together with the big percentages of pine pollen indicates forest on the spot. No sedimentation is found from the rest of the oak period. The sand and the mud indicate the formation of the Filso lake. Sand as well as mud contains pollen of beech which show—just as the diatomite—that the lake was dammed up in the beech period. The diagram does not tell in what part of that period it took place.

An investigation of the drifted sand brought a solution. In many places, for instance along the roads, sections were seen in the sand. It shows at the top a layer of light yellow sand of a thickness varying from few centimeters to two metres. It rests on a layer of humified sand with washed out grey sand below and below that again a hard and well

developed hard-pan. These layers have been formed in drifted sand, which means that below the upper layer of drifted sand from the beech period is found still a layer of drifted sand. This lower layer seems to have formed the big hills which later have been covered by the younger layer.

West of Lystbæk gaarde and west of Madum aa and south of the road from Ulfborg to Thorsted peat was cut in a hollow between the dunes; the peat was covered by the upper layer of drifted sand, in all 2 m. thick. In a place where the covering sand was taken away the following section was found:

- 0-20 cm. red, crumbling *Sphagnum* peat.
- 20-80 cm. dark brown strongly humified *Sphagnum* peat.
- 80-95 cm. brown forest peat with bark of birch.
- 95 cm. + sand.

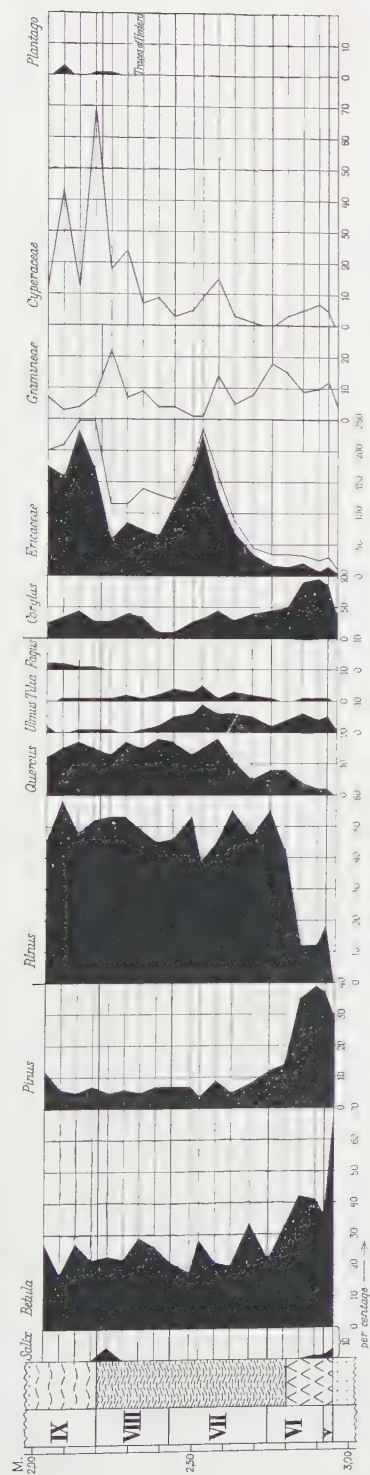
The border between drifted sand and the underlying peat was very distinct and the peat was without sand. Much wood and many roots of pine were lying on the surface. The workers told they were all from the bottom of the peat.

The diagram shows that the forest peat is contemporaneous with the forest peat in the valley at Filso, which is from the pine period. The many remains of pine show that also on this place there has been pine forest. The humified *Sphagnum* peat is from the oak period. Alder and birch have dominated but elm and lime have been at the place beside oak. *Calluna* has started to play a part. Beech enters when the formation of the younger *Sphagnum* peat starts. After a short while the drifted sand killed the vegetation by covering the bog with two meters of sand.

The diagram shows that the upper layer of drifted sand was formed in the beginning of the beech period. The peat is situated between the younger and older layer of drifted sand. The bottom peat with 3% *Salix*, 68% *Betula*, 29% *Pinus* and 35% *Corylus* belongs to zone V. After all the lower layer of drifted sand is late glacial. This dating is in accordance with the works of V. MILTHERS (1925) and KNUD JESSEN (1939) and with my own investigations from the heath-plains connected with Stora and Karup aa (H. JONASSEN, 1935, 1948 and 1950), where Kragso, Birkso and Bedso is situated in shallow basins undoubtedly wind-scooped; they are all formed in late glacial time.

The history of the area south east of Ulfborg must be the following:

When the soil in late glacial time was sufficient dry and still before the vegetation was strong enough to cover the surface and protect it a strong



# FEN IN THE VALLEY OF MADUM AA AT FILSÖ



Fig. 1.



sand-drift took place and the immense dunes north and south of Madum aa were formed.

With the beginning of the forest period the movement of the sand stopped. Forest covered the area. The forest peat in the two investigated localities shows that pine forest has covered the lower areas of the dunes and the river valley. Later alder and birch have been the most common trees accompanied by elm, oak and lime. Through the pine period and the beginning of the oak period NAP-values are not bigger than 50 % (NAP-pollen is all pollen except from trees and from hazel and the percentage is taken of the sum of tree-pollen). These figures show that forest has played an important part also on the higher areas. This supposition is supported by the fact that the peat is *Sphagnum* peat, not forest peat from the beginning of the oak period. It means that the tree-pollen is not local. It is to assume that alder and birch have grown in the wet basins while pine and oak have managed to live at dry slopes.

At the end of zone VII pollen of *Calluna* gets more common; *Calluna* covers the bog and is presumable getting common in the dry forest. The *Calluna*-percentages seems to tell that the vegetation is a mixture of forest and heath with the last as an important part. This vegetation continues to the beginning of the beech period when sand-drift starts and covers all with a carpet of sand.

If the dating of the lower layer of drifted sand to late glacial time is right the formation of hard-pan at the top of it cannot be late glacial. The diagram indicates that the formation started in the later part of the oak period when *Calluna* took over a dominant place.

The above mentioned investigations took place in 1937. I want here to render my heartiest thanks to Professor KNUD JESSEN who secured the economic basis for the work. I also want to thank Mr. ALFRED KAAE, teacher at Kronhede Skole for assistance during my visit in the area.

### Literature.

- JESSEN, KNUD, 1939: In V. MILTHERS: Geologisk Kort over Danmark. Kortbladet Brande. D. G. U. I. Række. Nr. 18.
- JONASSEN, H., 1935: Et pollendiagram fra Karupfladen. – Bot. Tidsskr. 43.
- 1935: Har Karup hedeblade været skovklædt? – Nat. Verden. 19.
- 1948: In THERKEL MATHIASSEN: Studier over Vestjyllands Oldtidsbebyggelse. Nationalmuseets Skrifter, Arkæologisk-Historisk Række, II.
- 1950: Recent Pollen Sedimentation and Jutland Heath Diagrams. Dansk Botanisk Arkiv, 13, 7.
- MILTHERS, V., 1925: Geologisk Kort over Danmark. Kortbladet Bække. D.G.U. I. Række. Nr. 15.

# The *Stratiotes* Lakes in Kittilä (Finnish Lapland) as a Floristic and Quaternary Problem

By MAUNO J. KOTILAINEN

HJELT & HULT (1885, p. 143) finding *Stratiotes Aloides* in 1877 at the confluence of the Rivers Aakenus and Ounasjoki in Kittilä, Finnish Lapland, could not foresee the real importance of their discovery.

SAMUELSSON (1934, p. 145) was the first to assess the finding at its true importance: "Dass auch in der Jetztzeit sehr eigentümliche Verhältnisse in Seen von Finnisch-Lappland vorhanden sind, geht u. a. daraus hervor, dass eine so wärmeliebende Pflanze wie *Stratiotes aloides* bei Kittilä (67°40' N. Br.) leben kann, während sie in Schweden nicht nördlicher als im Hälsingland (61°46' N. Br.) vorkommt." This statement of SAMUELSSON's gives the gist of the question of its distribution. Why is it that eutrophic submerged macrophytes, especially, are found growing in Northern Finland at the present days while some of them are missing completely in Central and Northern Sweden.

It has since been established that *Stratiotes* grows in Kittilä on a much more extensive area. The first find, i. e. that of HJELT and HULT, is from the Ounasjoki River, the later ones without exception from east of the Ounasjoki, along the systems discharging into the River Ounasjoki or into the River Kitinen. It does not, however, occur in river water, cf. Fig. 1.

The first additional data were published by SANDSTRÖM (1926, p. 54), who announced at the same time that *Stratiotes* is collected in the spring in great quantities as auxiliary fodder for cattle. It is consequently well known popularly as "kievana", which is an obvious loan word from Lappish.

About its use as fodder MARISTO (1941, p. 202) states the following:

"Wenn die im Sommer zusammengebrachten geringen Heuvorräte beim Fortschreiten des Winters zu Ende gehen, begibt man sich auf den See und holt sich



Fig. 1. The *Stratiotes* area in Eastern Kittilä (Finnish Lapland).  
Lakes underlined and numbered.

- |                   |                     |                   |
|-------------------|---------------------|-------------------|
| 1. Juhmusjärvi.   | (= Julmajärvi).     | 2. Kelontekemä    |
| 3. Kuolajärvi.    | 4. Särkijärvi.      | 5. Pälkättijärvi  |
| (= Torasjärvi).   | 6. Säynäjärvi.      | 7. Majavajärvi.   |
| 8. Nunarajärvi.   | 9. Iso Hirvasjärvi. | 10. Sinermajärvi. |
| 11. Sotkajärvi.   | 12. Jeesiöjärvi.    | 13. Hautajärvi.   |
| 14. Souvalojärvi. | 15. Rastinjärvi.    | 16. Vuomasjärvi.  |

das Futter mit rechenartigen Geräten durch zuvor an erfahrungsgemäss reich-  
ergiebigen Stellen in das Eis gebrachte Öffnungen heraus”.

The writer came across *Stratiotes* in connection with his bog investiga-  
tions in Kittilä in the summer of 1934. In Lake Jeesiöjärvi he saw the  
species in deep layers but intermixed with other species, e. g. *Potamogeton*  
*zosterifolius* and *Myriophyllum spicatum*, which HJELT and HULT (1885)  
had not encountered at all in their area of investigation.

When MARISTO started to investigate the Finnish lake types the writer recommended the disjunctive *Stratiotes* lakes of Kittilä as an investigation area. By then the present writer knew of well over ten such lakes. MARISTO (1941) investigated only four of them but with notable floristic results, (l. c., pp. 107–109 and the table attached). He also described a special *Stratiotes* lake type (l. c., pp. 197–205) the characteristics of which are described in the following quotation:

“auch dort kann man Gewässer begegnen, die in bezug auf ihre Makrophytenvegetation noch als eutroph angesprochen werden müssen. — — —. Diese Eutrophie tritt uns — — — nicht im Helophytenbestand entgegen, denn die Strenge des Winters und in Zusammenwirkung damit die Gefrierschäden sorgen dafür, dass die Bestände stets klein und lichtwüchsig bleiben. Unter der Wasseroberfläche hat sich dagegen eine um so üppigere Wasservegetation entwickelt, die überdies zur Hauptsache aus lauter Eutraphenten zusammengesetzt ist. Zur Entstehung einer solchen Vegetation so hoch oben im Norden sind natürlich ganz besondere edaphische Voraussetzungen nötig und solche gibt es auch in der Tat hier und da im Bereich der basischen Schiefer Finnisch-Lapplands.

Den Namen habe ich diesem Seetyp nach einer seiner Charakterarten gegeben. *Stratiotes aloides* ist eine Art elektrolytreichen Wassers und tritt in ähnlich beschaffenen Gewässern auch in den übrigen Teilen des Landes reichlich auf. — — —

Die Zahl der eutraphenten Arten schwankt 4 und 5 und mit Ausnahme von *Lemna minor* handelt es sich um Wasserblattkräuter, von denen zwei, nämlich *Stratiotes aloides* und *Myriophyllum spicatum*, auf allen vier Seen anzutreffen sind” (l. c., p. 197–198).

“Im Sotkajärvi und im Hautajärvi gab es — — — ziemlich reichlich *P. zosterifolius*. Eine besondere Erwähnung verdienen ausserdem *P. filiformis* und *Ceratophyllum demersum* aus dem Hautajärvi, speziell die letztgenannte Art, die in Finnland bisher nicht jenseits des Polarkreises angetroffen wurde, hier aber recht reichlich auftritt. — — —

Nirgends in der Literatur habe ich geeignete Vergleichspunkte zu jenen extrem alkalischen Seen Lapplands finden können. Aus unserem Lande sind solche Gewässer noch nie beschrieben worden und auch im reichhaltigen lappländischen Material LOHAMMAR's (1938) fehlen sie völlig” (l. c., p. 203–204).

MARISTO is quoted at such length because he fell in the war (1941) after publishing his academic dissertation, and his plant specimens, later lost, were not presented to our museum. (Later a part of the specimens were obtained for the museum.) This explains why HULTÉN (1950) makes no mention of MARISTO's notable finds which extend the distribution mapped in the atlas. MARISTO's finds are given full credit in the Kittilä studies by J. SALONEN and the present writer.

The writer had not intended to publish a paper on the *Stratiotes* lakes in Kittilä known to him, but in 1950 an “accident” made them even more



Fig. 2.  
*Najas flexilis* (WILLD.)  
 ROSTK. & SCHM. Finnish Lapland, Kittilä.  
 Leg. 19.8.1950 M. J.  
 KOTILAINEN.

interesting than before. In August 1950 the writer was in Kittilä in the *Stratiotes* region engaged in bog investigations, especially in the bogs skirting Pälkättioja. The writer took a plant sample either from the Pälkättioja brook or the nearby Ahvenjärvi brook which he assumed *mirabile dictu* to be a "*Nitella*" and which, without closer scrutiny, he put between the leaves of his map-case. The sample subsequently turned out to be *Najas flexilis* (teste G. MARKLUND), cf. Fig. 2. The writer's excuse is that the possibility of finding the species so far north (c. 600 km. NNW. of the previous northernmost find, Särkijärvi Lake at Liperi, and approx. 100 km. to the north of the northernmost fossil occurrence near Pello on the River Tornionjoki, cf. Fig. 3 and BACKMAN, 1948 and 1950) seemed out of question. In addition to the location of the site of the find the discovery is noteworthy in that it was made in running water perhaps for the



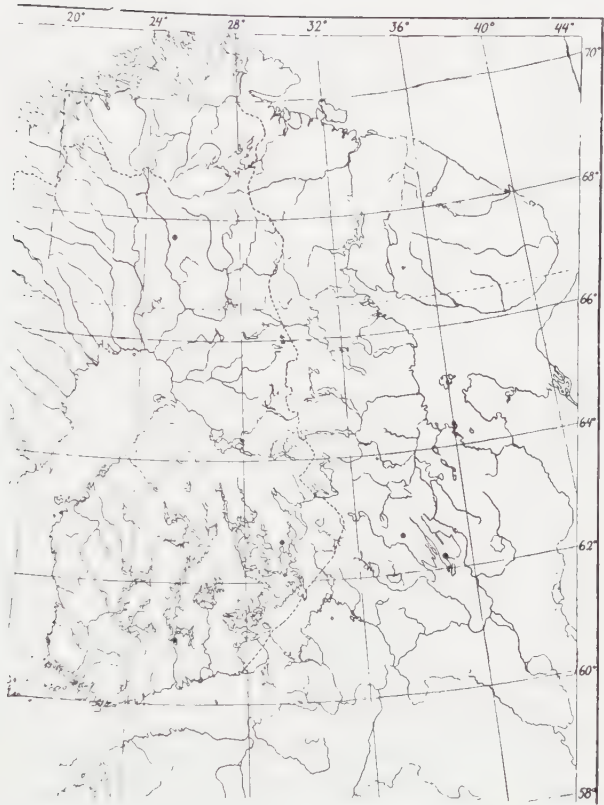


Fig. 3.  
Recent *Najas flexilis*  
in Fennoscandia ori-  
entalis.

first time in Europe. The sample was small. The writer re-visited the site in August 1951 but the brooks were so full, thanks to the ample precipitation of the autumn, that further searching for the plant proved futile. The observation has been made on Lake Vesijärvi in Southern Finland that at least *Najas tenuissima* may disappear for years from a certain site to re-appear later in the same spot.

It is only natural that the problem of the *Stratiotes* lakes in Kittilä has become more complex through the finding of *Najas flexilis*. MARISTO's explanations alone no longer suffice. The first question which arises is why *Stratiotes* does not occur in the neighbouring parish of Kolari, SW. of Kittilä, where the basic schist area continues. In the east and south-east the species does not occur until the well-known disjunctive and relict areas of Kuusamo and Kainuu, where again extensive basic schists and carbonates occur, cf. Fig. 4. The absence of *Stratiotes* especially in the neighbourhood of the River Muoniojoki at Kolari and on the

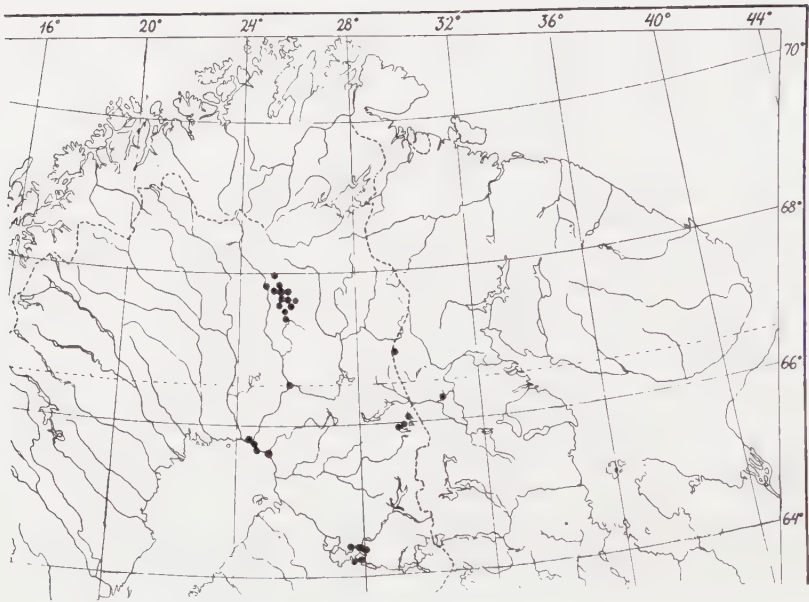


Fig. 4. *Stratiotes Aloides* L. in Northern Fennoscandia orientalis.

All the 18 dots in Kittilä are not denoted.

Swedish side is strange. The phenomenon is not, however, the only one of its kind.

In his study on the distribution of the meso-eutrophic bog flora in Northern Finland (KOTILAINEN, 1951) the writer found that a notable decline is observable in the frequency of some species such as *Saussurea* (op. c. p. 144–147) when proceeding from Kittilä to Kolari although the same vegetation and the zone of Karelids extends to Kolari and, according to the present data, some distance on the Swedish side. The writer was unable at the time to give a satisfactory explanation for this phenomenon. But moving now to the Swedish side, across the Tornio-Muoniojoki rivers, we shall find an obvious solution from Norrbotten and, simultaneously, perhaps an explanation for even deeper problems.

When examining HULTÉN's atlas (1950) the writer hit upon a significantly recurrent distribution feature of several species. A considerable number of eutrophytes, both bog and water plants, in the North-Finnish schist regions even rather common species like *Eriophorum latifolium* (cf. KOTILAINEN, 1951, map on p. 156) seemed to stop at the Tornio-Muoniojoki rivers or in their vicinity. The writer first attributed this to an error on the part of the editors of the atlas, but he recently received from

Dr. H. LUTHER confirmation that *E. latifolium* has not been found in Northern Sweden further west of Kolari than the neighbourhood of Kiruna (cf. HULTÉN, 1950, map 284).

In addition to *Eriophorum latifolium* such significant bog species as *Carex appropinquata*, *C. diandra*, *C. tenuiflora*, *C. panicea*, *C. flava*, *Paris quadrifolia*, *Orchis strictifolia*, *Gymnadenia conopsea*, *Coeloglossum viride* and *Listera ovata* (cf. HULTÉN, 1950, maps: 328, 329, 353, 383, 402, 504, 516, 532, 535, 541; KOTILAINEN, 1951, p. 156–162) stop, according to recent reports, at Tornio-Muoniojoki, approximately where the *Stratiotes* lakes lie, i. e. at the Swedish frontier or, very seldom, just across it.

In the writer's opinion there are only three possible explanations for this phenomenon. First, that Norrbotten has been much less thoroughly investigated floristically than Finnish western Lapland (Kolari, Muonio, Kittilä); second, that Norrbotten is considerably more barren than the Finnish side; third, that there is some flora-historical and at the same time Quaternary reason which has prevented the species from crossing "the Rubicon". BACKMAN's (1948, p. 39) conclusion makes vivid reference to the third explanation: "... dass aus Nordschweden nur ein einziger Fossilfund (*Najas flexilis*) vorgebracht worden ist trotzdem sich die Anzahl der nördlich Luleå untersuchten Vorseen auf 42 beläuft."

It is obvious that all three reasons contribute to the distribution pattern, but it is the third, i. e. the Quaternary, that is the most decisive.

It is true that Norrbotten may be one of Sweden's most poorly investigated regions, but floristic studies exist on Pajala, opposite Kolari (BIRGER, 1904). Norrbotten also has extensive barren areas, but the schist area of Alatornio extends on the Swedish side as far as the River Kalix. Further, the geological map of the Pajala region (Geologisk karta över Pajalafältet) by TRYGGVE ERIKSSON, i. e. of the area investigated by BIRGER, was printed in 1953 although the explanations have still to appear. According to the map the schists extend at least some 60 km. west of the Muoniojoki. Tärändö e. g. is in the centre of an extensive gabbro field, effusive greenstone occurs in long veins and there is also limestone in many places between Lombolovaara and Rismela (Muoniojoki), that is over a distance of some 35 km. The area is thus not barren throughout, especially not in the floristically best-investigated district of Norrbotten. Considering this, especially the distribution of the bog species needs re-investigation, although the absence of *Stratiotes* in Norrbotten obviously is certain.

The writer's actual "awakening" came when comparing HULTÉN's distribution maps with SAURAMO's (1940, p. 120, 124) maps of the late

glacial period, at which he had previously looked shivering mentally at the thought of open waters with floating icebergs and tundralike earth, a barrier to hydrophytes requiring a certain warmth. But then the idea came to him that perhaps those waters were not icy, at least not throughout, for melting ice water cannot cool a warm water for long periods today (although on the other hand, the same streams reduce the salinity of the water in the most northern part of the Gulf of Bothnia). The *Stratiotes* lakes are today about 60–80 km. from the one-time edge of the glacier in the region of the Muonionjoki to which the waters and the uncovered earth reached at a time when the ice still covered the “Lake Finland” north of Salpausselkä. But in that case, if those wide open waters, studded then with islands, which are at the present day hills, served as bearers of diaspores, the hydrophyte element in question, could at least in part, be much older, some 4,000–6,000 years, than hitherto believed, in other words considerably older than the Ancyclus-Littorina thermal period. Prof. M. SAURAMO has accepted the writer’s theory adding that some 11,000 years ago, during the Alleröd period (cf. JESSEN, 1949) of about 2,000 years, it was fairly warm in Finland, and especially in North Finland the ice-free water and uncovered earth extended much farther westwards than in Central Finland. Dr. E. HYYPPÄ, too, agreed with the writer’s conclusion and declared that he had found old river banks near Pello, east of the Torniojoki.

In the writer’s opinion this is the most likely explanation of the present-day occurrence of *Najas flexilis*, *Stratiotes* and *Ceratophyllum* in Kittilä, naturally supposing that those waters could not have been very saline or were possibly even fresh. In these circumstances the recent occurrences of our eutrophic hydrophyte flora could, even in the north, to a considerable extent be relicts<sup>1)</sup> from the climatically favourable Alleröd period surviving until now only in basins and in groups of basins rich in electrolytes or in slightly brackish waters. There are no “sehr eigentümliche Verhältnisse in Seen von Finnish-Lappland” as SAMUELSSON wondered in 1934, but “in den nacheiszeitlichen Klima von Finnish-Lappland” as one could continue. The ice cover particularly in the *Stratiotes* areas was relatively thin in the late glacial period thanks to the continental climate, since the large masses of snow, which stopped at the Scandinavian

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<sup>1)</sup> Naturally not always “in situ” in the very same spots where they now grow. They have migrated, as in the Gulf of Finland, in the wake of the receding sea. In Northern Finland they have survived only in areas where waters rich in electrolytes have been available continuously, as in Kittilä and Kuusamo. But in the south, e. g. in Lake Vesijärvi, near the city of Lahti, they are also local relicts.



mountains and were necessary for the formation of a thick ice blanket, were no more successful at that time than today in reaching Finland (Sauramo, orally). According to our Quaternary geologists, these Alleröd waters probably connected up in the east with the south as far as the area of the present Gulf of Finland, Lake Ladoga and Lake Onega. It is precisely on this eastern semicircle that our rare eutrophic hydrophytes mainly occur. Norrbotten has been left without some species of our eutrophic hydrophyte flora since there too, except perhaps in the eastern parts, the ice was a barrier at this early era. This recent flora, completely absent at least according to present knowledge in Norrbotten, is represented in the *Stratiotes* lakes by *Najas flexilis* (Fig. 3), *Potamogeton lucens* (and *P. Zizii*), Fig. 5, and *Ceratophyllum demersum* (Fig. 6) in addition to *Stratiotes*. These lakes also have other submerged eutrophytes such as *Potamogeton zosterifolius*, (Fig. 7) *P. filiformis* (Fig. 8), *Myriophyllum spicatum*, *M. verticillatum*, cf. Table 1. The relict nature of these eutrophytes cannot be regarded as a matter of certainty.—*Potamogeton zosterifolius* apparently has a wider spreading capacity than the species of the *Stratiotes* group; this is indicated by the 4 findings made in Norrbotten (HULTÉN, 1950, map 109) and two findings on a low island (Hailuoto) in the north of the Gulf of Bothnia (cf. Fig. 7). *P. filiformis* also has been found twice and the species certainly possesses a good spreading capacity; it occurs abundantly e. g. in Jämtland even in fresh bog ditches, but in Kittilä its disjunction (cf. Fig. 8) is obviously old. Its distribution in Scandinavia perhaps points to hibernation in refuges. The remaining *Myriophyllum spicatum* and *M. verticillatum* will not pass in the manner of *Stratiotes* as indicators of the Alleröd thermal era for the following reasons: the former has either young occurrences or at least occurrences pointing to hibernation in Northern Norway and in the Torneå-Lapland; the latter, on the other hand, probably came to the north in the Ancylus-Littorina era, i. e. the second thermal period, cf. HULTÉN, 1950, maps 1297 and 1298. Some other species such as *Potamogeton rutilus* (Fig. 9), *P. pectinatus* (a very rare species in Fennoscandia orientalis as an inland species, cf. HULTÉN, 1950, map 102) and the hybrids *P. pectinatus* × *vaginatus* (in Kuusamo and Onega) and *P. filiformis* × *vaginatus* are obviously relicts on the eastern "semicircle" of the Alleröd era but have not been found in the *Stratiotes* waters of Kittilä.

Attempts to explain the recent occurrences of eutrophic hydrophytes have evidently, at least in Finland, been too exclusively based on the assumption of a single thermal period (Ancylus-Littorina) in spite of the



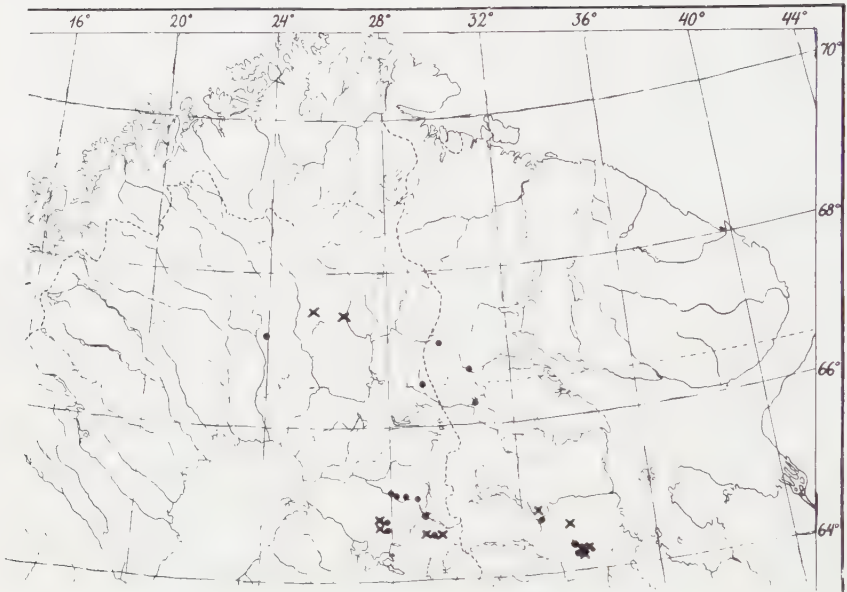


Fig. 5. *Potamogeton lucens* L. (●) and *P. Zizii* MERT. et KOCH (×) in Northern Fennoscandia orientalis. The seashore occurrences have been omitted from Fig. 5.

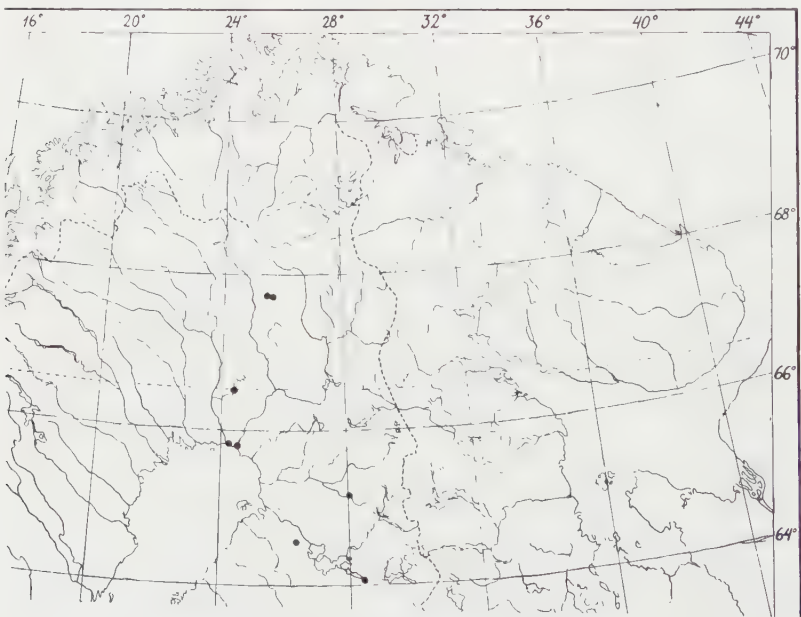


Fig. 6. Recent *Ceratophyllum demersum* L. in Northern Fennoscandia orientalis.

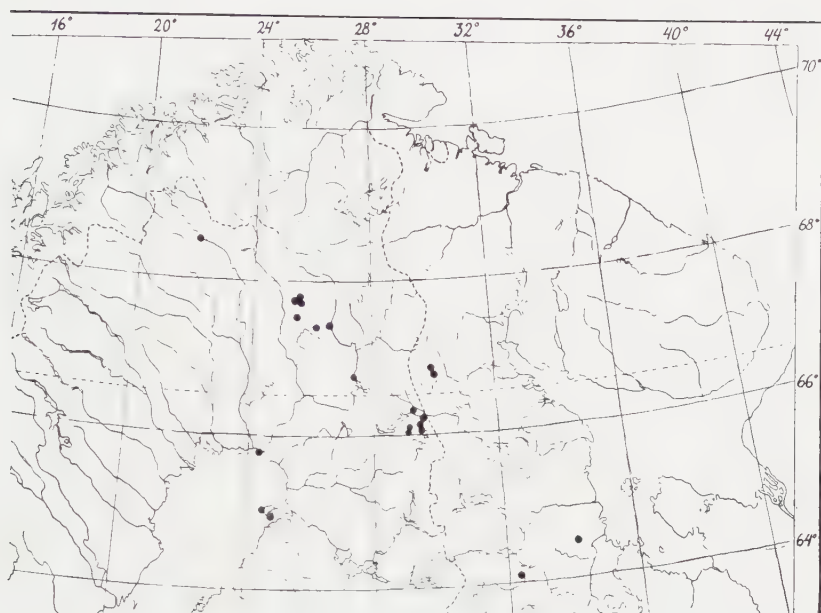


Fig. 7. *Potamogeton zosterifolius* SCHUM.  
in Northern Fennoscandia orientalis.

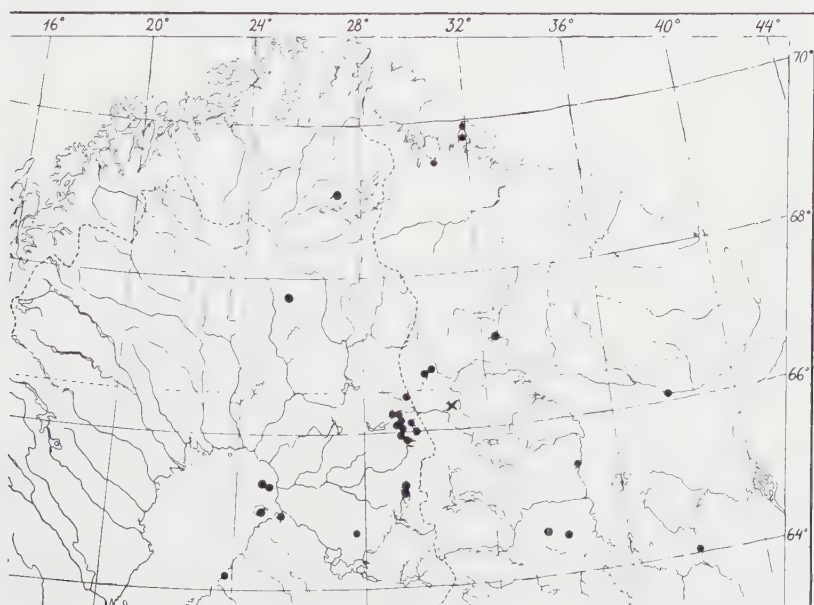


Fig. 8. *Potamogeton filiformis* PERS. (●) and *P. filiformis* × *vaginatus* (×)  
in Northern Fennoscandia orientalis.

Specimens from the localities shown in Figs. 5–8 deposited in the Herbarium  
Musei Fennici.

Table 1. Species list of the *Stratiotes* lakes studied floristically in Kittilä according to MARISTO, SALONEN and KOTILAINEN, cf. Fig. 1, p. 142.

Species	Lake						
	2. Kelontekemä	15. Rastinjärvi	Kuivajärvi <sup>1)</sup>	12. Jeisöjärvi	13. Hautajärvi	8. Nunarajärvi	11. Sotkajärvi
<i>Potamogeton praelongus</i> . . . . .	+	+	—	+	+	+	+
<i>P. Zizii</i> . . . . .	+	—	—	—	—	—	—
<i>P. zosterifolius</i> . . . . .	+	—	—	+	+	—	+
<i>P. filiformis</i> . . . . .	—	—	—	—	+	—	—
<i>Lemna trisulca</i> . . . . .	+	—	—	—	—	—	—
<i>L. minor</i> . . . . .	+	—	—	—	—	—	—
<i>Stratiotes Aloides</i> . . . . .	+	+	+	+	+	+	—
<i>Ceratophyllum demersum</i> . . . . .	—	—	—	+	+	—	—
<i>Myriophyllum spicatum</i> . . . . .	+	+	+	+	—	+	+
<i>M. verticillatum</i> . . . . .	—	+	+	—	—	—	—

<sup>1)</sup> Kuivajärvi. Not underlined, or numbered! Situation SE of and close to Rastinjärvi (15).

fact that an older period, the Alleröd, has obviously also affected their distribution and occurrence in the far north. Their fossils are distributed in the muds, possibly interspersed by the “*Dryas*” layer. The effect of this younger *Dryas* period cannot, however, have been destructive to these species.

In the winter these submerged “live fossils” have been protected by the ice cover. Only real annuals have failed to stand the shortening of the growth season in unfavourable times. But *Najas flexilis*, for instance, might possibly be, at least in the north of Finland, a species germinating in the autumn; i.e. it could be a winter annual (Prof. K. JESSEN’s assumption in a letter) which would eliminate the detrimental effect of the short growing season as does the long light period of the Lapland summer in the clear waters of the *Stratiotes* lakes.

Why could not the time of arrival of eutrophic hydrophytes in general in southern Sweden and Finland’s eastern and northern parts be placed at least approximately in the same older thermal period, especially if we consider that in Sweden and in southwestern Finland the earliest melting of the ice occurred approximately from south to north whereas in eastern and northern Finland the direction was east-west. The earliest history of the Finnish flora thus differs in many respects from the Scandinavian flora.

The ecology of the *Stratiotes* flora has already been accounted for by

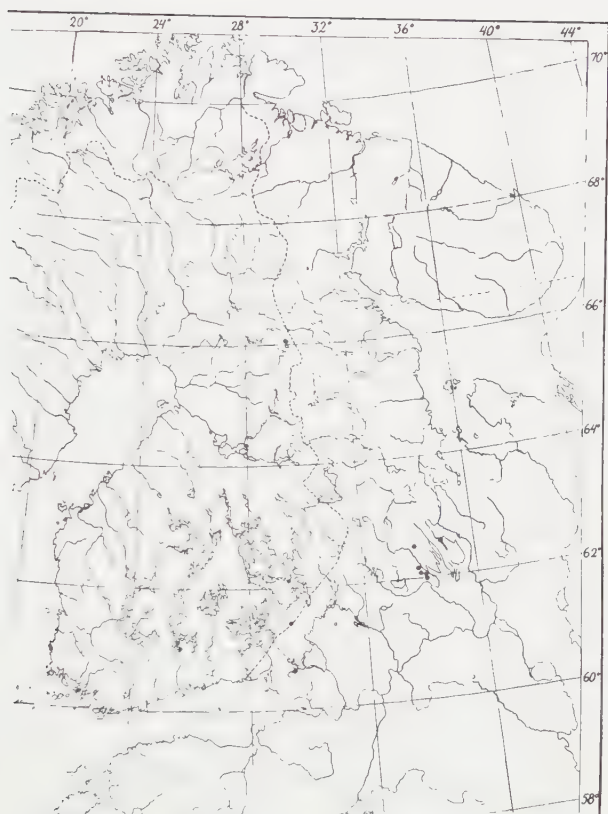


Fig. 9.  
*Potamogeton rutilus*  
WOLFG. in Fenno-  
scandia orientalis.

the waters rich in electrolytes in the schist areas of Kittilä where the supply of nutrients has been continuous. However, this has not been the case everywhere in North Finland, as can be judged from the fossil finds. *Ceratophyllum*, for instance, has previously had a much wider distribution (cf. HULTÉN, map 771) than *Najas flexilis* (cf. map 113) in North Finland (the atlas lacks the 4 fossil finds from the Åland Islands, cf. BACKMAN, 1948, p. 12). However, they both have a wide fossil distribution in comparison with their recent area. An endeavour has been made to explain the phenomenon but no final solution has as yet been found. However, even an amateur may have something helpful to add.

In HULTÉN's map the fossil occurrences of *Najas flexilis* are essentially in the wrong places, at least for Northern Finland (cf. BACKMAN, 1948, p. 13). The fossils are missing completely from the lower levels on the shore of the Gulf of Bothnia. Very few of them exist below the Littorina shore line (l. c.), the majority come from above it. It is a significant fact that they are also missing in the valley of the Kemijoki where, according

to SAURAMO (1940, p. 124), there was a lobe of ice at the time of the Yoldia Sea. Except in one locality (Övertorneå in Sweden) *Najas flexilis* has not spread across the Torniojoki to the Swedish side although the area of basic schist continues as far as the River Kalix. The reason must therefore be Quaternary.

The dying out of the species in many fossil localities in the extreme North, south of Kittilä, is in the present writer's opinion attributable at least in part to the deterioration of habitat conditions. Water of sufficient electrolyte content as in Kittilä has not been continuously available in the granite and gneiss areas in which the fossils have been found. The vigorous growth of peat in the subatlantic period resulted in the supra-aquatic growing over of basins, leaving only the fossils as relicts from bygone times. The eutrophic phase was short, as the thinness of the fossil layers indicates.

The growth of peat layers can be established in Kittilä too, though not under the influence of *Sphagnum fuscum*, for the electrolyte-containing water has in some way prevented the growing over of even small lakes, i. e. it has constituted an obstacle to a stifling *Sphagnum* invasion. Signs of the subatlantic period can also be seen in the *Stratiotes* lakes: in Kittilä they generally have peat shores, with the bottom covered by a thick mud layer, and they are usually small in area so that a part of the smallest basins may have become overgrown. However, the peat cover has then been of a better quality. Where *Stratiotes* grows in bigger lakes its communities are restricted to sheltered creeks for it cannot stand heavy sea conditions.

Our experienced and well-known paleobotanist Dr. A. L. BACKMAN told the writer that he has generally found it futile to look for "better macro-fossils" in the shore layering of eutrophic lakes. Thus he found no seeds of *Najas flexilis* in the layering of the *Stratiotes* lakes. Similarly he found no fossils of the species in the shore layering of Särkijärvi Lake in Liperi (Northern Karelia) in 1948, although he established in 1950 that the species grew in the middle of the lake on extensive areas. This may perhaps be accounted for in one of two ways: either the species grows only in the central parts of the basins or, while the basin is still open the oxygen concentration of the water causes the destruction of refuse and not until the lake is filled in and the acidity of the water below the surface has risen is the refuse fossilized.

In addition to the peat layers of bogs the recent vegetation and surface forms reflect the continuity of the eutrophic phase. In spite of the extreme northern situation of the *Stratiotes* lakes it is not the "Aapamoors" which prevail in the area (CAJANDER, 1913, pp. 73–80) but very extensive



so-called "birch fens" (cf. for instance LUKKALA & KOTILAINEN, 1951, pp. 6–7) which are characterised by park-like sparse birches. The birches are bushy, especially in the wettest parts of the bogs. Besides the birch, a very peculiar moss layer characterises these birch fens: *Drepanocladus vernicosus*, *Sphagnum teres*, *Paludella squarrosa*, *Calliergon* spp., with *Helodium Blandowii* often dominating. On the other hand the usual dominants of other fens, i. e. *Scorpidium scorpioides* and *Drepanocladus revolvens* (-*intermedius*) are missing completely and *Campylium stellatum* is very rare. The driest moss horizon is represented by *Sphagnum Warnstorffianum* and *Tomenthypnum nitens*, which do not, however, generally grow together, but mostly form pure communities. In the field layer *Saxifraga Hirculus* and *Carex diandra*, often also *Stellaria crassifolia*, are characteristic. It is true that these birch fens stretch beyond the boundary of the *Stratiotes* area and are also encountered on extensive areas at Kolari; they are even found to some extent on the Swedish side, at least in Pajala, but obviously on a decreasing scale, according to HULTÉN's (1950) maps.

We have thus by three different routes, i.e. via the continuous eutrophy of the peat layers of the bogs, second, the vegetation (birch fens) and third, the distribution of some interesting elements of the water and bog flora, arrived at the conclusion that the Tornio-Muoniojoki rivers are not only the boundary of the Finnish state, but at the same time constitute a significant borderline for the vegetation and flora, which is crossed only in exceptional cases. The basic reason for the formation of this boundary has been the essential difference of the Quaternary development on the two sides of the frontier. Naturally we must not forget the importance of the edaphic factors which explain the fact that the eutrophic phase has continued for thousands of years.

The present paper is not based on the writer's own Quaternary studies but on a field botanist's knowledge of the *Stratiotes* area and on the known recent distribution of the eutrophic hydrophyte flora. Their recent area is difficult to explain except by falling back on the old, climatically favourable Alleröd period. This view is also supported by the recent distribution of the southern element of land plants beyond the Alleröd eastern semi-circle far to the north to the peninsulas of Kola and Kanin: cf. for instance *Gagea lutea*, *Anemone nemorosa* (HULTÉN, 1950, maps 495, 791 and also KALELA, 1943, 1944, 1949).

The writer has not discussed the possible transport by birds of hydrophyte diaspores, which would have been unnecessary especially in regard to *Stratiotes*. Only in Rovaniemi is it found, as having spread along the Ounasjoki, cf. Fig. 14, and along the Kemijoki toward its delta. Spreading

by birds must not be overemphasised for the *Najas* family either. Thus *Najas tenuissima*, which arrived from the east, evidently stopped in Finland in the same Alleröd period. It would be very peculiar indeed if birds had been capable of spreading diaspores to the very places, and only to those places, where the recent occurrences of the species can most naturally be accounted for by the Quaternary history.

In addition to the persons mentioned in the text the author has obtained help, data and advice from the following persons: Dr. EVA THERMAN, Prof. V. AUER, Prof. A. KALELA, Mr. J. SALONEN and Mr. J. LONNAKKO.

### References.

- BACKMAN, A. L., 1948: *Najas flexilis* in Europa während der Quartärzeit. Acta Bot. Fenn. 43. Helsingforsiae.
- 1950: *Najas tenuissima* (A. Br.) Magnus einst und jetzt. Comm. Biol. Soc. Scient. Fenn. 10, 19. Helsingfors.
- BIRGER, S., 1904: Vegetationen och floran i Pajala socken med Muonio kapellag i arktiska Norrbotten. Ark. f. Bot. 3, 4. Stockholm.
- CAJANDER, A. K., 1913: Studien über die Moore Finnlands. Acta Forest. Fenn. 2, 3. Helsingforsiae.
- ERIKSSON, TRYGGVE, 1953: Geologisk karta över Pajalafältet. Stockholm.
- HJELT, HJ. & HULT, R., 1885: Vegetationen och floran i en del af Kemi Lappmark och Norra Österbotten. Medd. Soc. F. Fl. Fenn. 12. Helsingfors.
- HULTÉN, E., 1950: Atlas över växternas utbredning i Norden. Stockholm.
- JESSEN, K., 1949: Studies in late Quaternary deposits and florahistory of Ireland. Proc. of the r. Irish Acad. 52, B:6. Dunkalk.
- KALELA, A., 1943: Die Ostgrenze Fennoskandiens in pflanzengeographischer Beziehung. Veröff. d. Instit. Rübel in Zürich 20. Bern.
- 1944: Systematische und pflanzengeographische Studien an der Carex-subsektion Alpinae Kalela. Ann. Bot. Soc. 'Vanamo' 19, 3. Helsinki.
- 1949: Mistä ja milloin Suomi on saanut kasvistonsa? Eräitä ääri viivoja. Suomen Luonto 1949. Helsinki.
- KOTILAINEN, M. J., 1951: Über die Verbreitung der meso-eutrophen Moorpflanzen in Nordfinnland. Ann. Acad. Scient. Fenn. A, IV, 17. Helsinki.
- LOHAMMAR, G., 1938: Wasserchemie und höhere Vegetation schwedischer Seen. Symb. Bot. Upsal. 3, 1. Uppsala.
- LUKKALA, O. J. & KOTILAINEN, MAUNO, J., 1951: Soiden ojituskelpoisuus. Helsinki.
- MARISTO, L., 1941: Die Seetypen Finnlands auf floristischer Grundlage. Ann. Bot. Soc. 'Vanamo' 15, 5. Helsinki.
- SAMUELSSON, G., 1934: Die Verbreitung der höheren Wasserpflanzen in Nord-europa. Acta phytogr. Suecica 6. Uppsala.
- SANDSTRÖM, V., 1926: Vesisaha (*Stratiotes aloides*) karjanrehuna Kittilässä. Luonnon Ystävä 30, 2. Helsinki.
- SAURAMO, M., 1940: Suomen luonnon kehitys jääkaudesta nykyaikaan. Porvoo/Helsinki.

## Characterization of Plant Groups by Area Coverage

By MOGENS KØIE

A group of plants, for instance from a particular region or plant community, is generally characterized according to the distribution of the species that constitute the group by stating the percentage distribution of the species over a number of area types (WANGERIN, 1932; STEFFEN, 1935; MATTHEWS, 1937; MEUSEL, 1940, 1943; BÖCHER, 1943, and others). However, it will always be a matter of personal estimate how to group the area types, how large to make them and what principles to apply. Similarly, the assignment of species to the various area types chosen will also generally be a matter of personal judgment. Strictly speaking, each species has its own area type because no two species have the same area, but the comparatively small number of "types" to which, for reasons of clarity, such examinations have to be restricted necessarily render each type somewhat heterogeneous.

Another considerable drawback of this method of characterizing a plant group according to the distribution of its species is its dependence on the geographical point taken as the starting point. Some species described in England as "eastern" may, for instance, be called "Central European" in Denmark; if the starting point is further east, such discrepancies become even more flagrant. It is difficult to avoid describing the area type by means of relative indices, but the avoidance of such relative indices is imperative if the method is to be universally applicable. Hence, it will be preferable to take the distribution of the individual species as the direct basis rather than using a term which in any circumstances must be very summary.

In this article the characterization of plant groups by means of area coverage will be discussed in the light of a few examples. This method is objective inasmuch as it does not presuppose assignment of individual

species to any arbitrary area type, and also because it enables us to apply all available knowledge about the distributions of the species in the plant group.

The first example is the vegetation on a littorina slope at Strandkær, Mols (East Jutland). The incline was approximately 35° facing south east. In the analysis of the vegetation (by RAUNKJÆR's circling method) in Table 1 the figures show frequency percentages; species that were not encompassed by the circles are indicated by '+’.

Table 1.

<i>Achillea millefolium</i> .....	60	<i>Hypericum perforatum</i> .....	20
<i>Agrostis canina</i> .....	20	<i>Hypochoeris maculata</i> .....	+
<i>Agrostis tenuis</i> .....	20	<i>Lotus corniculatus</i> .....	+
<i>Anthyllis vulneraria</i> .....	+	<i>Luzula campestris</i> .....	30
<i>Arenaria serpyllifolia</i> .....	10	<i>Myosotis micrantha</i> .....	20
<i>Artemisia campestris</i> .....	80	<i>Ononis repens</i> .....	40
<i>Astragalus glycyphyllos</i> .....	+	<i>Phleum nodosum</i> .....	10
<i>Avena pratensis</i> .....	100	<i>Pimpinella saxifraga</i> .....	80
<i>Campanula rotundifolia</i> .....	30	<i>Plantago lanceolata</i> .....	10
<i>Carex hirta</i> .....	40	<i>Sedum acre</i> .....	20
<i>Carex verna</i> .....	30	<i>Silene nutans</i> .....	100
<i>Dianthus deltoides</i> .....	20	<i>Thymus serpyllum</i> .....	+
<i>Erophila verna</i> .....	+	<i>Trifolium arvense</i> .....	+
<i>Festuca ovina</i> .....	20	<i>Trifolium procumbens</i> .....	10
<i>Festuca rubra</i> .....	100	<i>Veronica chamaedrys</i> .....	+
<i>Galium verum</i> .....	90	<i>Veronica verna</i> .....	+
<i>Gnaphalium arenarium</i> .....	+	<i>Vicia cracca</i> .....	+
<i>Hieracium pilosella</i> .....	10	<i>Viscaria vulgaris</i> .....	+

Distributional maps were drawn for the 36 species from the plant community (and of the species included in the following examples). For the distribution in Scandinavia HULTÉN's atlas (1950) was used; for the other areas such maps as could be found in literature were used, but many of the distributional maps had to be drawn on the basis of records found in floras, etc. They do not claim to be very accurate, especially not for the Mediterranean area.

The boundaries of the areas for the 36 species were mapped on one base map and lines (isochores) drawn for 25, 50, and 75 per cent area coverage. The results appear in Fig. 1 in which the outermost hatched portion shows the area within which between 25 and 50 per cent of the species occur; the middle portion shows the area with 50–75 per cent

coverage, and the innermost (densest) hatching indicates an area coverage of 75 per cent or more. Besides, the curve delimiting the 90 per cent area coverage is shown on this map.

The number of species in a plant group can be so high that it may involve technical difficulties to map the area coverage. In such cases it would be an advantage if it were sufficient to map only part of the group; the selection would then have to be independent of the criterion on which the group was constituted.

It is quite feasible to handle 36 species, but in order to ascertain the extent to which a sample of the species in the above example is representative of the whole group, it was divided into three sub-groups of equal size. The 24 species encompassed by the circles constituted two of the sub-groups which were arranged alphabetically according to the species names. Figs. 2 and 3 show fairly good conformity within these two groups and also with Fig. 1. The 50 per cent isochore in Fig. 2 would have been very nearly similar to that of Fig. 3 if the area around Trondheimsfjord had been considered as being continuous with the more southern range for only two of the three species involved (*Myosotis micrantha*, *Luzula campestris* and *Silene nutans*).

The third sub-group comprises the species from the supplementary flora list, i. e. species occurring comparatively sparsely in the plant community. The course of the isochores is very similar to that of the two other sub-groups, but the extent of corresponding area coverages is smaller. The 75 per cent isochore closely follows the course of the 90 per cent curve in Fig. 1. In other words: The extent of the 75 per cent area coverage of this sub-group is not larger than that of the 90 per cent area coverage for all the species in the community.

For comparison, the area coverage of the 12 species with the highest frequency percentages (100–30) has been mapped. Fig. 5 shows that the result is not very different from the map of all the species.

In this example, therefore, the sparsely occurring species are at least as indicative as the most frequent species.

Finally, the six annual plants have been mapped (Fig. 6), supplemented by the following six species from another analysis of a vegetation on the same slope: *Aira caryophylla*, *Cerastium semidecandrum*, *Medicago lupulina*, *Trifolium striatum*, *Turritis glabra*, *Vulpia bromoides*. The 50 per cent curve for Scandinavia takes the same course as the 75 per cent curve in the other maps, and the group generally shows a more Mediterranean-Atlantic tendency.

Plant groups of 12 species are probably the smallest groups that



Table 2.

<i>Achillea millefolium</i> .....	30	<i>Hieracium pilosella</i> .....	20
<i>Achillea ptarmica</i> .....	80	<i>Hypochoeris radicata</i> .....	10
<i>Agrostis tenuis</i> .....	80	<i>Leontodon autumnalis</i> .....	80
<i>Carex leporina</i> .....	20	<i>Luzula campestris</i> .....	60
<i>Carex oederi</i> .....	80	<i>Poa pratensis</i> .....	10
<i>Carex panicea</i> .....	70	<i>Potentilla anserina</i> .....	40
<i>Carex pulicaris</i> .....	10	<i>Prunella vulgaris</i> .....	100
<i>Carex stolonifera</i> .....	20	<i>Ranunculus bulbosus</i> .....	40
<i>Cerastium caespitosum</i> .....	10	<i>Ranunculus flammula</i> .....	10
<i>Festuca ovina</i> .....	10	<i>Rumex acetosa</i> .....	10
<i>Festuca rubra</i> .....	80	<i>Sieglingia decumbens</i> .....	100
<i>Hieracium auricula</i> .....	100	<i>Trifolium repens</i> .....	20

should be made the subject of area statistics, especially if the ranges of the species are very dissimilar; in that case the small number would make the course of the isochores somewhat accidental. The degree of importance to be attached to the comparatively small variations in Figs. 1-5 will best be seen by comparing these maps to maps of area coverages for other plant groups. A few examples will be discussed briefly.

Fig. 7 covers the species referred to in Table 2 from an analysis of the vegetation on a previously cultivated meadow at Strandkær. The soil was a 20 cm. layer of sandy humus (7-10 per cent loss on ignition) above sand, pH 5.7. Many of the species have wide ranges and the isochores are not likely to reveal any characteristic features.

Fig. 8 (Table 3) represents a plant community dominated by *Juncus squarrosus*, situated about 100 metres from the previous community. There was a layer of approximately 25 cm. sandy humus above sand; the loss on ignition was 32 per cent and pH 4.0. Fig. 9 (Table 4) is also from Strandkær. The site was flooded in winter. The soil was peat with a small amount of sand, to a depth of at least 50 cm.; pH was 5.7. The oceanic nature of both of these examples is particularly conspicuous in the 75 per cent isochore. A comparatively large part of the species represented in Fig. 9 have their northern limit just around the Gulf of Bothnia (at least 25 per cent, i. e. between the 50 and 25 per cent isochores). None of the species in Figs. 8 and 9 had the distribution curve along the southeastern coast of Norway that was characteristic of many (about one third) of the species in Table 1, recognizable in all the maps from that plant community (Figs. 1-5) through the course of the 75 per cent isochore.

Table 3.

<i>Agrostis canina</i> .....	100	<i>Hieracium pilosella</i> .....	10
<i>Agrostis tenuis</i> .....	80	<i>Hydrocotyle vulgaris</i> .....	100
<i>Anthoxanthum odoratum</i> .....	10	<i>Juncus squarrosus</i> .....	100
<i>Calluna vulgaris</i> .....	50	<i>Luzula campestris</i> .....	100
<i>Carex panicea</i> .....	10	<i>Pedicularis silvatica</i> .....	40
<i>Carex pilulifera</i> .....	40	<i>Potentilla erecta</i> .....	100
<i>Festuca ovina</i> .....	10	<i>Pteridium aquilinum</i> .....	10
<i>Galium saxatile</i> .....	100	<i>Viola palustris</i> .....	20

Table 4.

<i>Agrostis stolonifera</i> .....	80	<i>Hydrocotyle vulgaris</i> .....	70
<i>Carex oederi</i> .....	60	<i>Juncus articulatus</i> .....	100
<i>Echinodorus ranunculoides</i> .....	90	<i>Juncus bulbosus</i> .....	100
<i>Galium palustre</i> .....	100	<i>Myrica gale</i> .....	20
<i>Glyceria fluitans</i> .....	30	<i>Potamogeton oblongus</i> .....	80
<i>Heleocharis palustris</i> .....	90	<i>Ranunculus flammula</i> .....	100
<i>Helosciadium inundatum</i> .....	100		

Fig. 10 is a map of the following 12 forest plants which require a soil with a high content of clay:

<i>Bromus ramosus</i>	<i>Gagea lutea</i>
<i>Carex silvatica</i>	<i>Mercurialis perennis</i>
<i>Circaea lutetiana</i>	<i>Platanthera chlorantha</i>
<i>Corydalis cava</i>	<i>Primula elatior</i>
<i>Corydalis fabacea</i>	<i>Pulmonaria obscura</i>
<i>Festuca gigantea</i>	<i>Veronica montana</i>

They all occurred at a content of more than 32 per cent silt-clay (particles < 0.02 mm.) and not at a content of less than 20 per cent silt-clay in Table 7 (KOIE, 1951). The 25 per cent isochore follows the boundary of *Quercus robur*, at least in North and West Europe. On this map the 100 per cent curve is drawn. It is approximately concentric with the 75 per cent curve, centered on Central Europe.

For comparison, a group of 12 species have been mapped which according to KOIE (1951, Table 5) are restricted to the most sandy soil found in woods. Nearly all of them are facultative forest plants and most of them are characteristic mor plants. Fig. 11 shows that the 50 per cent isochore passes north of Scandinavia and that the area for 75 100 per cent has a distinctive northwestern location. The species are:

<i>Anthoxanthum odoratum</i>	<i>Melampyrum pratense</i>
<i>Carex montana</i>	<i>Poa pratensis</i>
<i>Deschampsia flexuosa</i>	<i>Pteridium aquilinum</i>
<i>Galium saxatile</i>	<i>Trientalis europaea</i>
<i>Luzula pilosa</i>	<i>Vaccinium myrtillus</i>
<i>Majanthemum bifolium</i>	<i>Vaccinium vitis-idaea</i>

Finally, a map has been drawn (Fig. 12) of the area coverage of 12 species which are characterized through their occurrence in Denmark where they are found only in the comparatively dry area around the northern end of the Great Belt and some of them also in the low-precipitation belt through North Sealand, at Møns Klint and in the coastal regions of Bornholm island:

<i>Anthericus ramosus</i>	<i>Potentilla arenaria</i>
<i>Astragalus danicus</i>	<i>Scabiosa canescens</i>
<i>Cynanchum vincetoxicum</i>	<i>Scabiosa columbaria</i>
<i>Inula conyza</i>	<i>Seseli libanotis</i>
<i>Kohlruschia prolifera</i>	<i>Tetragonolobus maritimus</i>
<i>Medicago minima</i>	<i>Vicia tenuifolia</i>

Most of the above species have been mapped for Denmark (JESSEN, 1931 and 1935, EGHOLM, 1951, HANSEN, 1951).

The north and northwestern curves are close and almost parallel; to the south and southwest they are far apart. The area of the 75–100 per cent area coverage is divided into two parts: a small one around the Great Belt and a larger area which is characterized by its eastern range and, to the north, includes Öland and southern Gottland. This part has its centre in Eastern Central Europe within which all the species occur.

Even though this article is not intended to elucidate special problems of plant geography, it may be appropriate to refer to the previously mentioned hypothesis (KOIE, 1954, p. 179) that the occurrence of the majority of the "Great Belt plants" in Denmark is attributable to a particularly favourable light climate. They are limited to areas with relatively many hours of sunshine; they grow preferably in open vegetation and on slopes facing the sea (or the lakes) where the light is intensified by reflection.—Several of the species (among those listed in the example: *Astragalus danicus*, *Scabiosa columbaria* and *Seseli libanotis*) belong to the fairly large group of eastern species which have an isolated distribution in England where they grow only on lime. This is generally ascribed to the history of the vegetation (most recently by PIGOTT and WALTERS,

1954), but the lime hills with their open vegetation and light-coloured ground have particularly light local climates which, undoubtedly, should be borne in mind when discussing the occurrence of these species in their westernmost distributional areas.

The foregoing examples are all restricted to plants occurring in Denmark. In all cases except the last one, this common criterion has caused the highest area coverages to be in Denmark and the countries nearest to Denmark. However, a comparison of the maps nevertheless reveals major differences in the course of the isochores for the various plant groups. It might no doubt have been more satisfactory also to have included Asia, but for many species it was difficult to establish the eastern limit and as this study is essentially a discussion of the method, it was found preferable to make a more detailed examination of northwestern Europe, from where the most complete and reliable information about the distribution of the species is available.

For purposes of comparison it is necessary to draw the limits at definite percentages of area coverage and 25, 50, and 75 per cent have been used; the number of species in the group does not have to be a multiple of 4; the isochores may be drawn between area boundaries for the individual species.

It might be tempting to exclude the plants with the widest distributions from the groups in order to prevent them from blurring the picture. However, this would be a questionable procedure and it is also superfluous. The fact that a species has a wide distribution is, in itself, a characteristic feature and if there are specific area-characterizing species they will always be recognizable in the isochores, but in groups with many wide-ranging species the special course of these curves will only be apparent at high area-coverages. If the group consists almost entirely of species of a particular distribution type or with particular common distributional features this may become apparent already at the 25 per cent isochore.

The area of 100 per cent area coverage may in some cases result in a particularly distinctive characterization (Figs. 9, 10 and 12). Thus, the group is characterized by the quality that all the species are able to grow within that area. But while the 25, 50 and 75 per cent limits will not vary very much with the number of species in the group as long as that number is sufficiently large, the 100 per cent area is likely to decrease and approach the initial area when the number of species in the group increases. On the other hand, two species alone may be sufficient to reduce the area to a point.

In some cases, however, the high area coverages may not occur at all; this will happen if the occurrence of a species within a certain region is not part of the criterion on which a group was based. Examples of such criteria may be common morphological, anatomic or cytological features (the range of plant groups with different capacity of spreading, the ratio between diploid and tetraploid forms of closely related species, etc.) or a systematic relationship (e. g. *Verbascum*: MURBECK, 1939).—It should be noted, however, that if a plant group is based on the criterion that total areas of the species must be more or less equiformal (HULTÉN, 1937, 1950; RAUP, 1947) the grouping of the species is a subjective one which will reduce the possibilities of drawing conclusions on the basis of their area coverages.

Considerations based on knowledge of the distribution of the individual species in plant groups will, of course, not be rendered superfluous by the discussed method of regional-geographic characterization of plant groups. The method can only be used in contexts where it is of no importance which of the species are included in the various area coverages. In theory, plant groups whose species have concentric areas might give the same isochores as those shown in the examples.

## References.

- BÖCHER, T. W., 1943: Nordische Verbreitungstypen. — Svensk Bot. Tidskrift 37: 352–370.
- CAIN, S. A., 1947: Characteristics of natural areas and factors in their development. — Ecological Monographs 17: 185–200.
- EGHOLM, B., 1951: The distribution of the Umbelliferae within Denmark. (Danish with English summary). — Bot. Tidsskr. 47: 373–480.
- HANSEN, A., 1951: The distribution of the Caprifoliaceae, the Adoxaceae, the Dipsacaceae, and the Cucurbitaceae within Denmark. (Danish with English summary). — Bot. Tidsskr. 47: 481–510.
- HULTÉN, E., 1937: Outline of the history of arctic and boreal biota during the Quaternary period. — Stockholm.
- 1950: Atlas of the distribution of vascular plants in N.W. Europe. (Swedish with English summary). — Stockholm.
- JESSEN, K., 1931: The distribution within Denmark of the higher plants. II. The distribution of the Papilionaceae within Denmark. — Det kgl. danske Vidensk. Selsk. Skrifter, naturv. og mat. Afd., 9. Række, III, 2: 19–96.
- 1935: The distribution of Liliales within Denmark. (Danish with English summary). — Bot. Tidsskr. 43: 71–132.
- KØIE, M., 1951: Relations of vegetation, soil and subsoil in Denmark. — Dansk bot. Arkiv 15, 5.



- 1954: A self-recording light integrator and a portable integrator for light-percentage measurements. — *Oikos* 4: 178–186.
- MATTHEWS, J. R., 1937: Geographical relationships of the British flora. — *Journ. of Ecology* 25: 1–90.
- MEUSEL, H., 1940: Die Grasheiden Mitteleuropas. Versuch einer vergleichend-pflanzengeographischen Gliederung. — *Botanisches Archiv* 41: 357–519.
- 1943: Vergleichende Arealkunde, I–II. — Berlin-Zehlendorf.
- MURBECK, L. v., 1939: Weitere Studien über die Gattungen *Verbascum* und *Celsia*. — *Lunds Universitets Årsskrift*. N. F. 35.
- PtGOTT, C. D. and WALTERS, S. M., 1954: On the interpretation of the discontinuous distributions shown by certain British species of open habitats. — *Journ. of Ecology* 42: 95–116.
- RAUP, H. M., 1947: Some natural floristic areas in Boreal America. — *Ecological Monographs* 17: 221–234.
- STEFFEN, H., 1935: Beiträge zur Begriffsbildung und Umgrenzung einiger Florenelemente Europas. — *Beih. z. Bot. Centralbl.* 53: 330–404.
- WANGERIN, W., 1932: Florenelemente und Arealtypen. — *Beih. z. Bot. Centralbl.* 49.

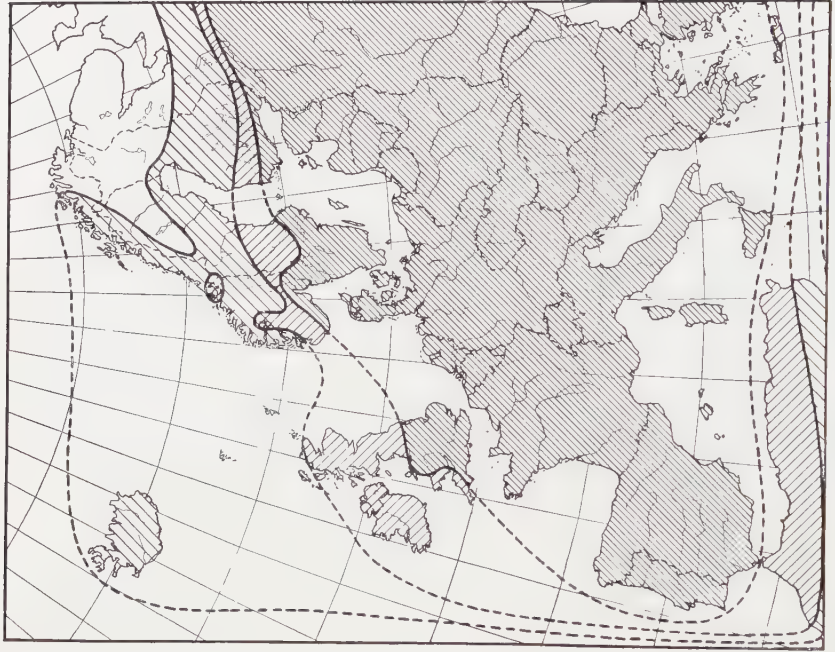


Fig. 2. The 12 species from Table 1 encompassed by the circle and with species names till 'o'.

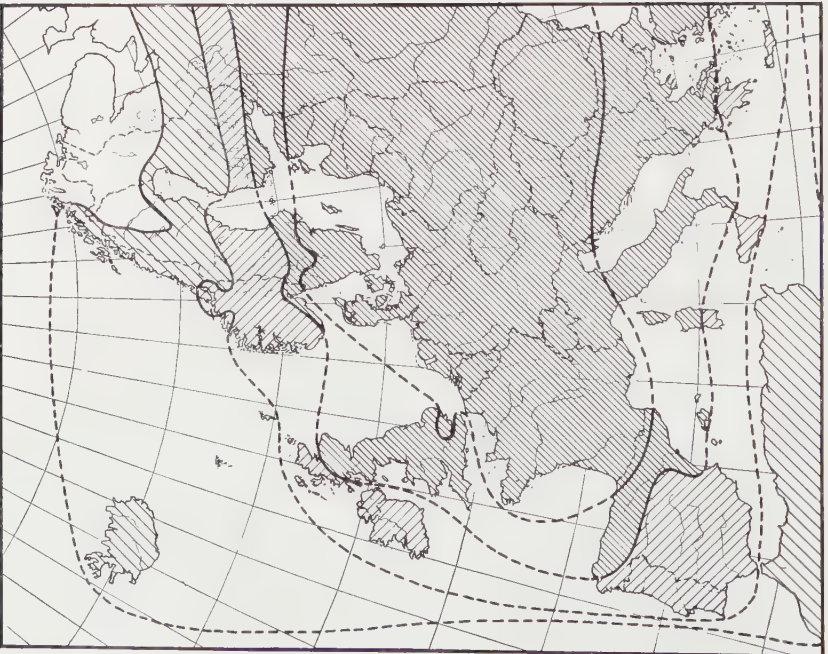


Fig. 1. All species from Table 1. In addition to the 25, 50, and 75 per cent isochores the 90 per cent isochore has been drawn.

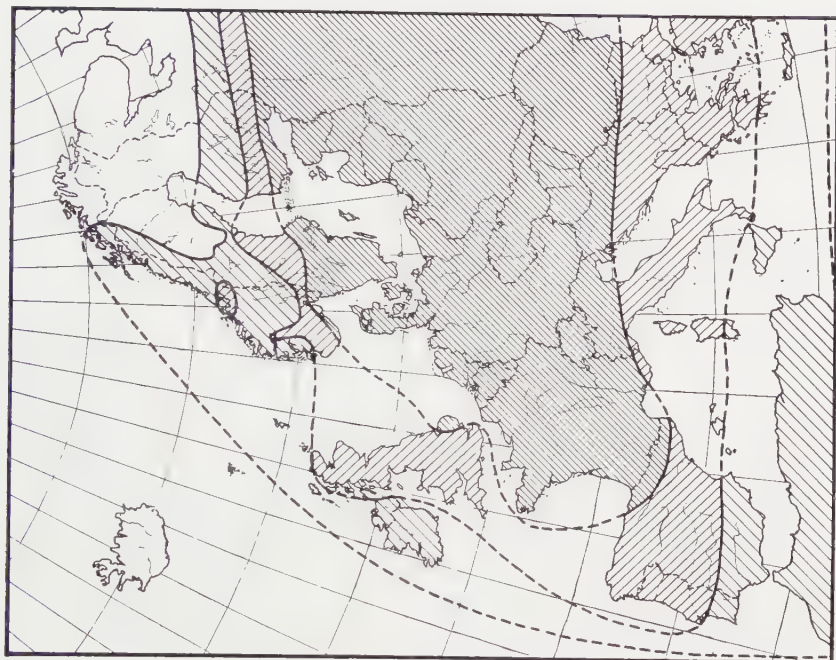


Fig. 4. The 12 species from Table 1 not encompassed by the circle.

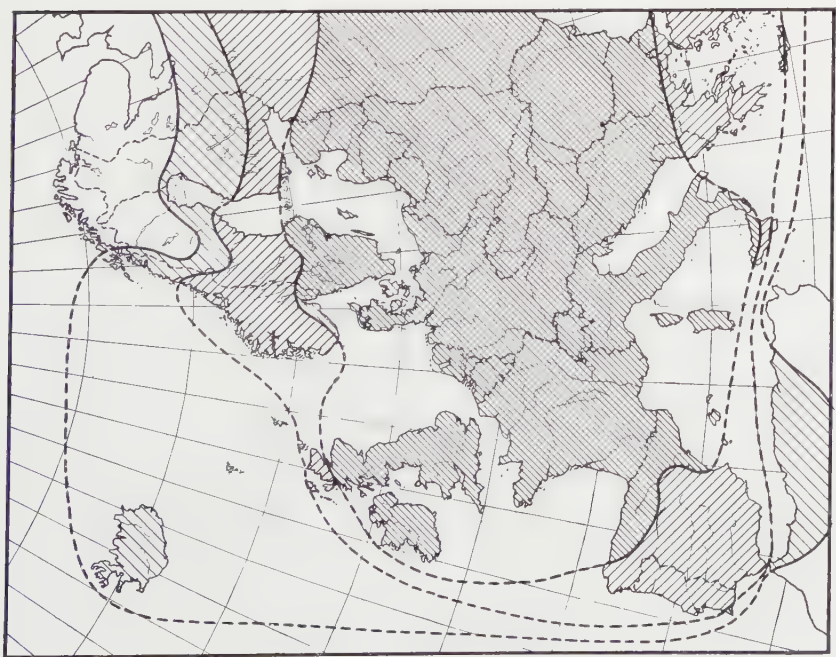


Fig. 3. The 12 species from Table 1 encompassed by the circle and with species names from 'p'.



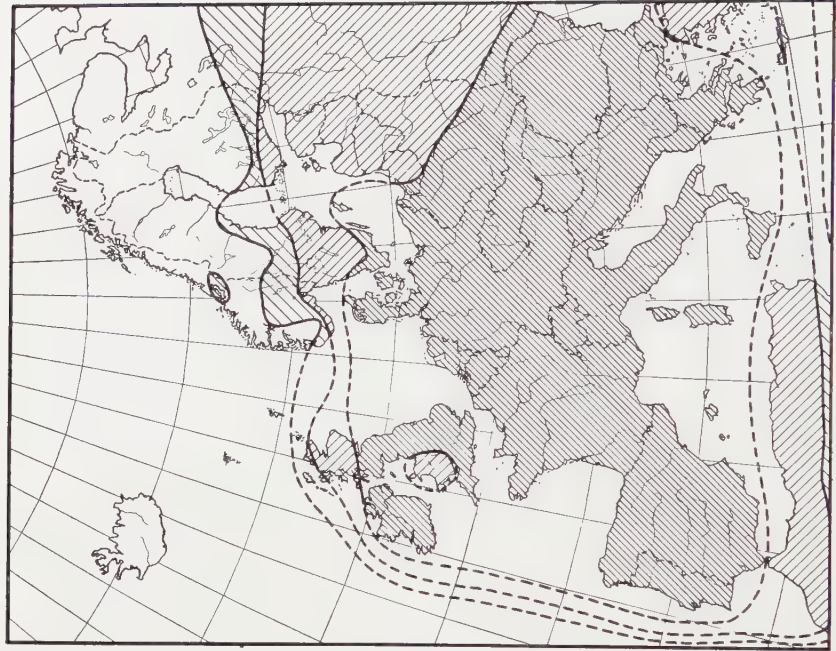


Fig. 6. The 6 annuals from Table 1, supplemented by 6 annuals from a similar plant community.

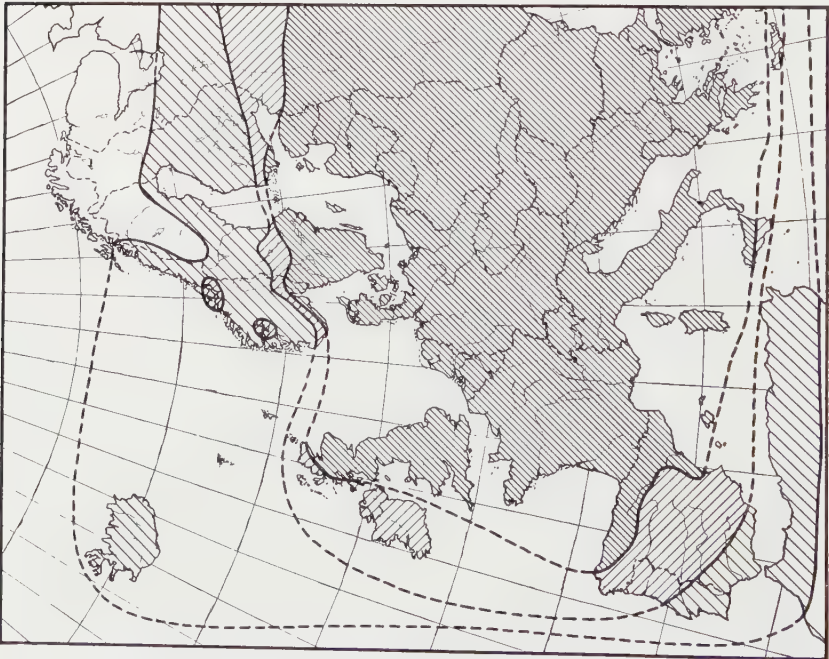


Fig. 5. The 12 species from Table 1 with the highest frequency percentages.

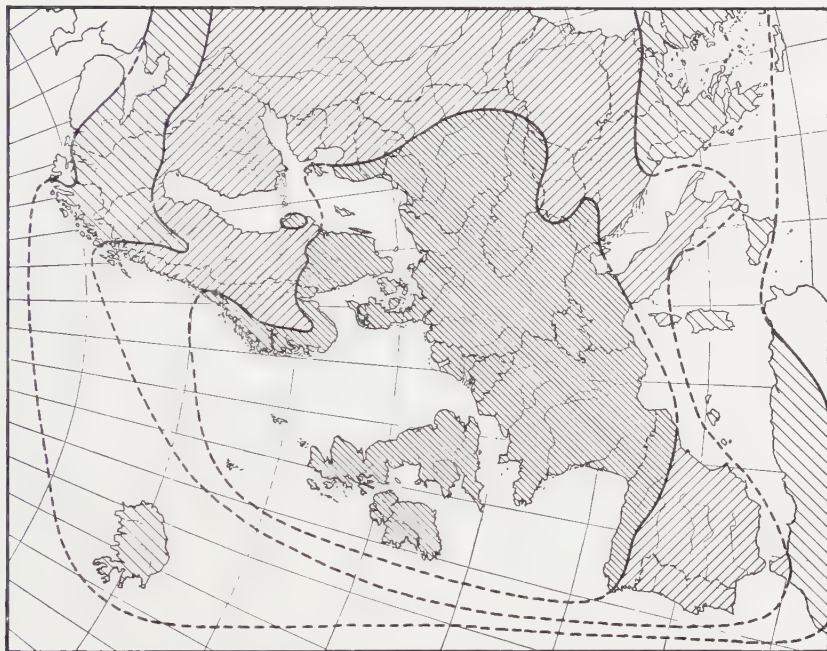


Fig. 8. The species from Table 3.

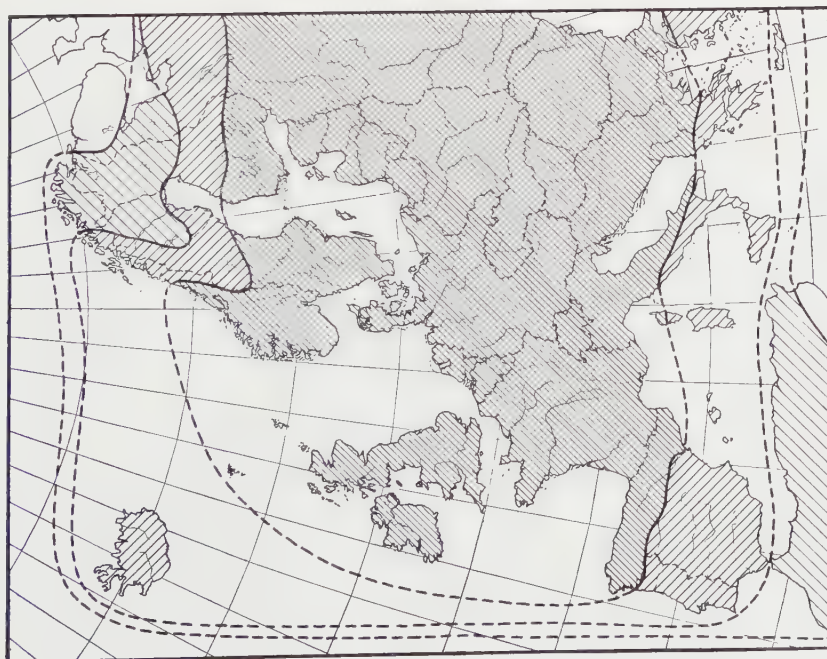


Fig. 7. The species from Table 2.



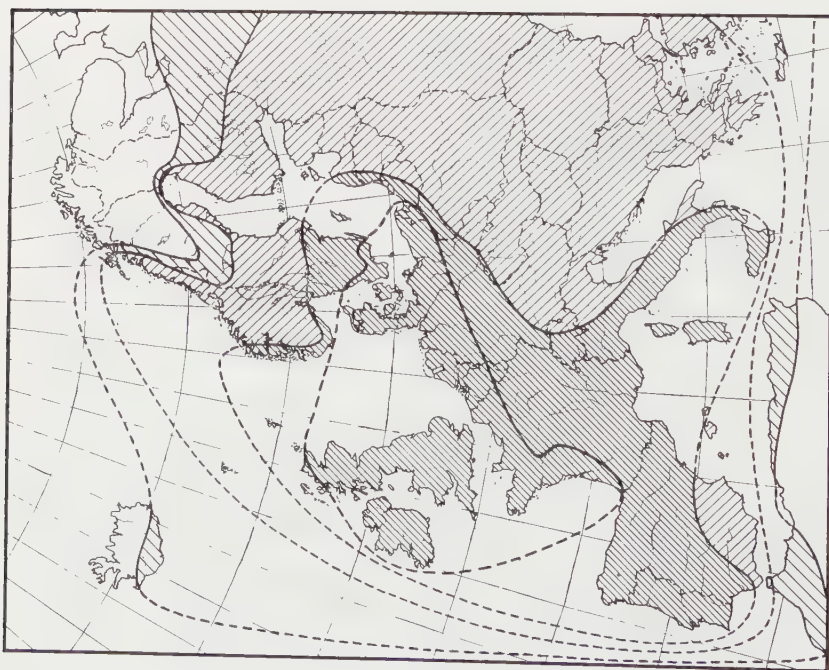


Fig. 9. The species from Table 4. The 100 per cent isochore has been drawn.

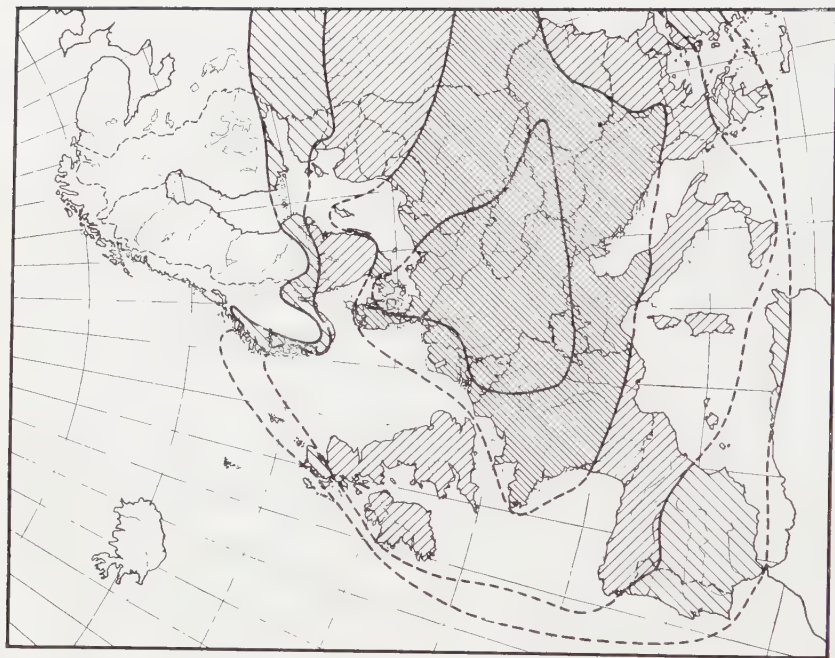


Fig. 10. Twelve forest plants from clayey soil. The 100 per cent isochore has been drawn.

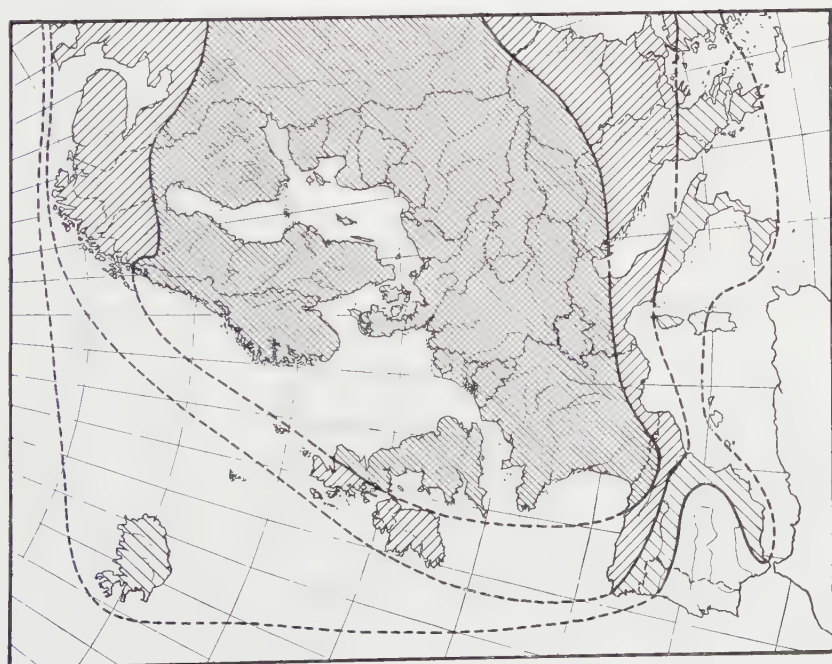


Fig. 11. Twelve forest plants from sandy soil.

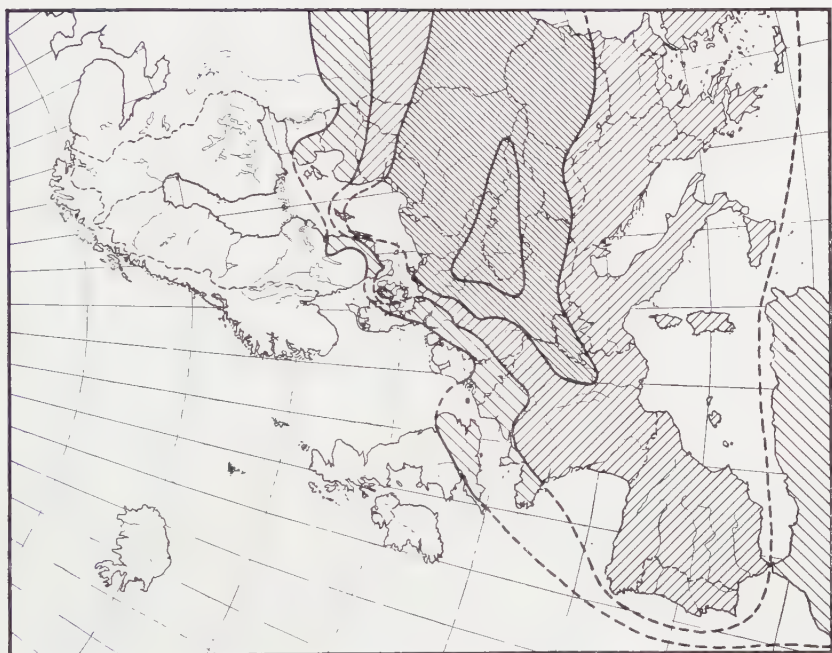


Fig. 12. Twelve species from localities with low precipitation.  
The 100 per cent isochore has been drawn.

## Dansk botanisk topografi og dens forhold til Kyllings *Viridarium*

Af JOHAN LANGE

Under udarbejdelsen af manuskriptet til Ordbog over Danmarks Plante-navne er mange gamle bøger blevet underkastet en fornyet gennemgang. Adskillige skrifter helt fra det 13. århundrede er blevet gennemsoget for plantenavne, og i de tidligere excerperede værker er talrige opslag gjort for at kontrollere, om senere forfattere og udskrivere har gengivet plante-navnene korrekt, og for om muligt at foretage en kontrolbestemmelse eller ombestemmelse af de ofte usikre navne i de gamle tekster og fortegninger.

Blandt disse på ny gennemgåede ældre værker indtager KYLLING's *Viridarium Danicum* fra 1688, som det vil være almindeligt bekendt i botanikerkredse, en særstilling på grund af sin rigdom på danske navne, og ganske særlig fordi det med hensyn til danske, vildtvoksende og forvildede planter er den første liste, der gør krav på nogenlunde fuldstændighed og nøjagtighed, disse ord taget med alt muligt forbehold over for den tids primitive opfattelse af artsbegrebet og over for datidens meget mangelfulde kendskab til floraen i store dele af landet og til mindre vigtige eller lidet distinkte plantearter i det hele taget. Det er en kendt sag, at KYLLING's *Viridarium* trods sine store mangler har kunnet give os mange vigtige oplysninger om floraen i Danmark for snart 300 år siden, ikke mindst i topografisk henseende. Mange danske florister og botaniske topografer har øst af KYLLING's viden, og meget vigtigt stof vil stadig kunne hentes i dette værk. Spørgsmålet er blot, om det vil være muligt at benytte KYLLING's materiale til bunds og uden risiko for fejl, og hvorvidt den især i Botanisk Tidsskrift udkomne del af den endnu uafsluttede topografiske behandling af plantefamilierne har draget fuld nytte af de sikre oplysninger hos KYLLING. Ingen af spørgsmålene kan besvares med et ubetinget ja, særlig ikke det sidste. Det er blandt andet



dette, der har vist sig ved den ovenfor nævnte nye gennemgang af bogen; og der kan derfor nu være anledning til at se lidt på, hvor meget der er gjort ud af KYLLING, og hvad der vil kunne gores for at undgå (alt for mange) fremtidige forsømmelser.

Man må selvfølgelig straks gøre sig klart, at mange af de pladser, KYLLING angiver som voksesteder, er „forsvundne” lokaliteter, angivelsen på kortet kan derfor kun markeres ved en „forhen-signatur” (ring); det gælder selvsagt især hans københavnske findesteder, der alle uden undtagelse må regnes med at være begravet under byen. Men også en lang række andre voksesteder er siden KYLLING’s dage forsvundet, f. eks. på grund af opdyrkning; det gælder således lokaliteter for *Botrychium lunaria*, der tidligere sikkert har stået adskilligt flere steder end i dag. På den anden side er det ikke udelukket, at flere af KYLLING’s planter på nu ukendte voksepladser må kunne findes på det eller de angivne steder, hvis der bliver søgt efter dem. KYLLING (eller hans meddelere) har f. eks. hjemsogt flere småholme, som næppe alle har været genstand for botanisk undersøgelse siden. KYLLING nævner Hyldeholm ved Lolland, Trolldholm, Vindholm, Ormholm, Kaninholm ved Haderslev, Ki(d)holm i Kolding Fjord o.s.v. Flere afsides beliggende steder kunne godt tænkes at give bekræftelse på KYLLING’s gamle angivelser. Ganske interessant i denne forbindelse er H. MORTENSEN’s beretning i Bot. Tidsskr. II (1867) s. 25–27 om hans eftersøgning af *Taxus baccata* på den af KYLLING angivne lokalitet („Udi i en Skov ved Fielderup”).

Inden vi nu går over til at se på enkeltheder i KYLLING’s topografiske afsnit, må det pointeres, at det ofte er forbundet med nogen vanskelighed at gøre sig klart, hvad KYLLING skriver om. Lokalitetsangivelserne er ofte ufuldstændige; af KYLLING’s ca. 188 lokaliteter er dog kun ca. 4 helt ubestemmelige; af resten er nogle få så summariske, at de ikke giver megen oplysning, f. eks. Udi Holsteen, Falster, Laaland, Møen; og andre er usikre. Værre er dog vanskelighederne med bestemmelsen af KYLLING’s latinske navne, især når det er sådanne, han selv lancerer. Til hans ros tjener, at autor i reglen anføres ved navne, han har andetsteds fra; således optræder CASPAR BAUHIN’s navn talrige gange (forkortet: C. B.). Derved lettes bestemmelsen væsentligt, idet LINNÉ som bekendt anfører de bauhinske (og andre) navne som synonymmer i Species plantarum, og en nogenlunde sikker bestemmelse ad denne omvej er muliggjort og først praktiseret af G. TYCHO HOLM; men alligevel støder man også her på vanskeligheder. KYLLING’s opfattelse af BAUHIN’s navne behøver ikke at være den samme som senere LINNÉ’s; der foreligger flere oplagte tilfælde af kyllingske (og linnæiske) fejlbestemmelser. KYLLING nævner f. eks. en

„*Lathyrus arvensis repens tuberosus* C. B.”, der ifølge LINNÉ er *L. tuberosus*; men når KYLLING angiver den som almindelig, må han med Jordnødder og Hedenødder (som han kalder sin plante) også have ment *L. montanus* eller muligvis kun denne. KYLLING's danske og tyske navne hjælper i mange tilfælde til en bestemmelse: Når en plante med navnet „*Lychnis segetum major*” i den danske rubrik kaldes „Klinte” og i den tyske „Korn-Rose, Korn-Neglein, Rade, Schwartz Coriander”, så er man jo ikke i tvivl om, at det er *Agrostemma githago*, der menes, selv om det sidste tyske navn egentlig tilkommer *Nigella (sativa)*. Når KYLLING side 116 opfører en „Stor Tand-Urt, Grosse Schuppenwurtz, Zahnkraut” og kalder den „*Orobanch radice dentata major* C. B.” med synonymerne „*Dentaria major* MATTH.” og „*Anblatum* DOD.”, så er der ingen som helst tvivl om, at det er vor *Lathræa squamaria*. Lige ovenfor har han „Et sær slags Tandroed, Ungemeine Zahnkraut”, som han på latin kalder „*Orobanch, qvæ Hypopytis dici potest*, C. B.” Heller ikke her kan der være tvivl om, hvad der menes; det er *Monotropa hypopitys*. Men når han foran denne anfører en „*Orobanch flore majore* J. B.” med synonymet „*Sqvamaria*” (uden autor) og de danske navne „Tandroed”, „St. Jørgens-Urt”, „Løwe-rumpe” og de tyske navne „Schuppenwurtz”, „Löwenschwantz”, „Zahnkraut”, „Sommerwurtz”, så tyder de først anførte to danske og det første og tredje tyske navn samt „*Sqvamaria*” på, at det er *Lathræa squamaria* igen, mens Loverumpe, Löwenschwantz og Sommerwurtz egentlig tilhører *Orobanch (major)* og altså peger i retning af denne. To ting synes dog at afgøre problemet: Det angivne blomstringstidspunkt „Maj” og oplysningen om, at det er en lægeplante, (fugleojesignatur, der angiver, at planten er „*usualis*”) kan ikke passe på *Orobanch*; derimod er *Lathræa* blevet brugt „som et sammensnerpende Middel” (HORNE-MANN) og imod krampe hos småbørn (TABERNÆMONTANUS m. fl.), og dens blomstringstid falder i april-maj. M. T. LANGE har altså næppe ret, når han (i 1859) bestemmer KYLLING's plante til *Orobanch elatior* 5: *O. major*. Denne forfatter har i sit ellers fortjenstfulde, lille værk, der især beskæftiger sig med bestemmelsen af KYLLING's navne, ofte regnet lovlig stærkt med, at KYLLING's artsliste måtte kunne bringes til at dække størsteparten af den liste, man på det tidspunkt kendte; det kan den ikke, hvad også JENS LIND peger på: „Man har ved de hidtidige Forsøg paa at udlægge KYLLING's Navne i alt for høj Grad stolet paa, at det var et ensartet og vel bearbejdet Materiale, man havde for sig” (LIND (1917) s. 12).

For ikke helt få planters vedkommende er det kun ved at tage alle KYLLING's sparsomme oplysninger med i overvejelserne muligt at komme



til et sikkert bestemmelsesresultat, andre er helt umulige. Men for nogle få planters vedkommende har det været gorligt at foretage bestemmelsen ad mere eksakt vej. Ved et lykkeligt træf er der nemlig blevet bevaret to samtidige herbarier. Det ene er den 30 bind store plantesamling, som JOCK. BURSER, en ven af CASPAR BAUHIN, samlede på sine talrige rejser i Europa og ordnede i Soro i 1630'erne. Det er forsynet med bauhinske navne og er blevet benyttet af M. T. LANGE (gennem E. FRIES, da herbariet beror på museet i Uppsala). Det andet herbarium er samlet af en af KYLLING's meddelere, som må formodes at have brugt de samme navne i sit herbarium og i sine antagelig 30-40 år senere til KYLLING indgivne meddelelser. Det drejer sig om apoteker C. HEERFORDT, der virkede i Nykobing Falster fra 1638 til 1660. På grundlag af HEERFORDT's herbarium, der sikkert er samlet på Lolland-Falster, og som er omtalt udførligt af JENS LIND (l. c.), har denne kunnet bestemme 30 af KYLLING's navne; og der er ikke særlig grund til at tvivle på denne metodes pålidelighed.

Holder vi os nu til de sikkert bestembare planter hos KYLLING og gennemgår den danske flora familie for familie, vil det, som allerede antydnet, vise sig, at der bliver enkelte ting at tilføje til de allerfleste af de før 1954 publicerede topografiske afhandlinger; de anføres i den rækkefølge, hvori de er udkommet; ved en senere lejlighed bringes de i 1954 trykte samt de endnu utrykte og ubehandlede familier.

I 1931 startedes udgivelsen af den topografisk-botaniske undersøgelses resultater med KNUD JESSEN: *The Distribution of the Papilionaceæ within Denmark*, der udkom som nr. III, 2 i *Det kgl. Danske Videnskabernes Selskabs skrifter*, afd. for naturvidenskab og matematik, 9. række. KNUD JESSEN benytter adskillige steder oplysningerne i KYLLING's *Viridarium*, og der er grund til at fremhæve, at professor JESSEN mere end nogen af de senere topografer har haft forståelse for KYLLING's og andre gamle floristers planteangivelser. Der er i virkeligheden intet at tilføje fra KYLLING med undtagelse af følgende: På side 96 som plante nr. 650 efter den af TYCHO HOLM indførte nummerering, der er benyttet af alle senere KYLLING-forskere, anfører KYLLING en „*Melilotus maritima foliis crassioribus*”, „Steenklever, som voxer ved Stranden”. Det er *Melilotus dentatus*; og KYLLING angiver, at den forekommer „Paa Elhorn ved Bognæs; ved Strandsiderne i Valdborg Herrit”. Elhorn er sikkert trykfejl for Elleore, en lille holm mellem Bognæs og Veddelev-halvøen lige n. f. Roskilde; på KNUD JESSEN's kort ligger de nærmeste findesteder omtrent 20 km i luftlinie fra Elleore (Holbæk-kanten, Frederikssund-egnen). Da Elleore imidlertid i det væsentlige består af strandvolde, der kan være nedbrudt og opbygget mange gange siden 1600-tallet, kan det

ikke ventes, at *Melilotus dentatus* har holdt stand på denne isolerede lokalitet. Ved et besøg den 3. juni i år eftersøgt den da også forgæves, hvorimod en anden af KYLLING's planter fra „Elhorn ved Roeskild" nemlig *Lepidium latifolium* fandtes i mængde. Da Elleore er denne plantes eneste voksested i hele det centrale, nordlige og vestlige Sjælland, er det klart, at Elhorn er (tryk)fejl for Elleore. „Valdborg Herrit" er naturligvis Voldborg herred ☉: den sydlige del af „Horns herred" († nogle sogne syd herfor). Det kan ikke undre, at *Melilotus* har vokset her tidligere, idet den fra nutiden er opgivet fra Eriksholm og Tusenæs. Men den gamle forekomst i Voldborg herred bør selvfølgelig også søges bekræftet.

Om *Ornithopus perpusillus* (nr. 761), som KYLLING i overensstemmelse med BAUHIN kalder „*Ornithopodium minus*", på dansk „Liden Fuglefoed", angives, at den vokser „I Aashærrit" og „ved Abor i Fyen". Det første sted er Ods herred, hvorfra den ikke ellers kendes; desværre er angivelsen meget løs, og da planten ikke er særlig konstant, vil en eftersøgning i det vidtstrakte Ods herred måske ikke lønne sig. Den anden lokalitet, identisk med Aborg n. ø. f. Assens, ligger inden for det område, hvor den ifølge TBU.'s angivelser er ret hyppig.

Som nr. 568 opføres en „*Lathyrus sylvestris major angustifolius*", „Store vilde Erter med smale Blade", „Udi Laaland". Den er af M. T. LANGE bestemt til *Lathyrus heterophyllus*, der for 100 år siden af E. MÖLLER-HOLST er fundet ved Råhave på Lolland. Dette kunne måske tyde på, at M. T. LANGE har ret, men da HEERFORDT i sit herbarium under det angivne navn har en ganske almindelig *L. silvester*, mener JENS LIND, at KYLLING må sigte til vor Skov-Fladbælg, selv om den er opført lige nedenfor (som nr. 569) under navnet „*Lathyrus major latifolius*", „Paa adskillige Stæder udi Skovene"; og deri har LIND sikkert ret; nr. 568 har altså blot været en særlig smalbladet form; dette passer især godt, hvis man tør regne med, at der ved nr. 569 er faldet er „*sylvestris*" bort lige efter *Lathyrus*. I alt har KYLLING lokalitetsangivelse til 24 papilionaceer.

Til KNUD JESSEN's topografiske behandling af liliiflorer (1933) er kun meget lidt at tilføje. KYLLING angiver *Narcissus pseudonarcissus* (719) som forekommende „Ved Assens i Fyen etc.", og da han også ellers er meget nøjeregnende med kun at medtage, hvad der virkelig er forvildet, foruden selvfølgelig de vildtvoksende arter, må man regne med, at den i det mindste har stået ved Assens, foruden på de på KNUD JESSEN's kort anførte steder. I parentes kan tilføjes at „vilde" Påskeliljer findes „i store mængder" både på Barsø og det østlige Lojt i Sønderjylland iflg. kronikken i Heimdal (Aabenraa) 7. jan. 1953. Den første forekomst, der iflg. samme meddelelse går mindst 80 år tilbage, blev kontrolleret i begyndel-

sen af maj 1953 af Afd. f. systematisk Botanik, Landbohøjskolen, ligesom der ved det samme besøg blev iagttaget ligeledes forvildede Vintergækker, *Galanthus nivalis* (fl. pl.) på Barsø.

KYLLING's *Allium*-arter er (med undtagelse af *A. ursinum* og *A. vineale*) for usikre til, at man tør slutte noget bestemt; hans 3 *A. montanum* turde være dels *A. oleraceum*, dels *A. scorodoprasum*, nærmere kan man næppe komme det; en af dem angives fra „Løge-Højen ved Ribe”; fra denne egn er ellers ingen Log-art angivet hos KNUD JESSEN. Det er formodentlig *A. oleraceum*, det drejer sig om; den har jeg i hvert fald set i et hegn i den vestlige udkant af Ribe i 1920'erne, mens Løghøjen har ligget i den østlige udkant, vist mellem seminariet og sygehuset. I alt har KYLLING lokalitetsangivelse til 13 liliiflorer.

Primulaceerne er behandlet af THORVALD SØRENSEN i 1933. Ca. halvdelen af arterne er som bekendt ganske almindelige, hvorfor KYLLING ikke angiver nogen lokalitet; andre er så sjældne, at han ikke har kendt dem. Af resten har han forsynet 5 med stedsangivelser. Findestederne ligger enten inden for planternes stadig gældende udbredelsesområde eller ganske nær dette. Det kan således ikke undre, at han har fundet *Primula farinosa* (1051–52) „paa Amager”, hvorfra den nu selvfølgelig er forsvundet; til TH. SØRENSEN's ti ring-lokaliteter for Melet Kodriver kan der altså føjes en ellefte og måske en tolvte, idet KYLLING's angivelse „Ved gammel Vartou” (ϝ: omtrent ved det nuværende Tuborg) ikke falder sammen med en af de ti ringe.

Også *Samolus valerandi* (60) kan få en ring-signatur på kortet et par kilometer nord for den, der i forvejen er anbragt (midt i København), idet KYLLING har fundet Samel „Imellem gammel Vartou oc Gyldenlund” ϝ: omtrent ved den nuværende Hellerup havn. Nok så interessant er hans fund af planten „ved Gisselfeld”. Til den række indlandslokaliteter, TH. SØRENSEN nævner, og hvoraf den nærmeste (Rislev) ligger ca. 15 km fra Gisselfeld, kan altså føjes KYLLING's fund, der i hvert fald indtil videre kun kan betegnes som et gammelt fund.

T. W. BÖCHER har taget sig af ericaceerne, vacciniaceerne og empetraceerne (1937). Til disse familier har KYLLING følgende at tilføje: *Andromeda polifolia* (212) fundet „ved Ravenstrup”, der antagelig er det sjællandske Ravnstrup mellem Skelby og Herlufmagle; fra disse kanter har KYLLING nemlig flere iagttagelser, derimod ingen fra omegnen af de nørrejske og falsterske Ravnstrup'er. *Erica tetralix* (286) fundet „ved Kiøbenhafn”; altså anbringer vi på kortet en ring her. *Oxycoccus quadripetalus* (1091) har KYLLING fundet „Udi Moratzer, ved Assens, paa den flyende Holm”. Denne noget uegale måde at angive lokaliteter på giver os bl. a. den

oplysning, at KYLLING kendte Tranebær som en ret almindelig plante, og at der på BÖCHER's kort kan indføjes en ring ved Assens; om voksestedet her netop var en flydende holm, eller om denne lå et andet sted i Danmark, fremgår ikke klart af stedet hos KYLLING; men terrænforholdene syd og sydøst for Assens kunne passe, og hans uforfælskede fynske måde at stave 'flydende' på kunne tyde på, at det er et sted, han kendte fra sin barndom, der jo netop tilbragtes i Assens. I alt har KYLLING lokalitetsangivelse til 7 arter i denne plantegruppe.

Juncaceerne (K. WIINSTEDT, 1937) var på KYLLING's tid så dårligt adskilt, at man ikke er i stand til at identificere ret mange arter hos ham, og da lokalitetsangivelserne er endnu færre, bliver der intet at tilføje.

Også polygonaceerne (JUL. GRØNTVED, 1939) er, bortset fra nogle almindelige arter uden særlig lokalitet, vanskelige at bestemme hos KYLLING. Dennes (lidt tvivlsomme) angivelse af *Polygonum bistorta* (788) „Paa Friderikshavns Volde" bekræftes af en opgivelse fra C. FERDINANDSEN („Plantagen") til TBU. Men planten figurerer også som nr. 113, hvor der ikke er nogen tvivl om dens identitet, og angives på dette sted fra Lolland, Roskilde og Vedbæk, hvoraf de to sidste er kendte lokaliteter; på Lolland synes KYLLING's fund bekræftet af en senere iagttagelse; men hvem der har ansvaret for, at GRØNTVED har kunnet anbringe en fugleøjesignatur ved Bandholm, har ikke kunnet oplyses.

*Hypericum*-arterne (AASE KOIE, 1939) er hos KYLLING næppe helt så moderne opfattet, som man af M. T. LANGE's bog kan få indtryk af. Vi må imidlertid her i det væsentlige indskrænke os til at omtale de arter, som KYLLING har ellers ukendte lokaliteter til; desværre er netop for Perikum-arternes vedkommende hans stedsangivelser til dels uklare. Der er dog vist ikke tvivl om, at „Løstrup" er Lystrup ved Slangerup i N. Sjælland, idet han andetsteds udtrykkelig skriver „Løstrup som er ved Slangerup". Det er *H. hirsutum* („Stor laaden Jordhumble", nr. 516), han har fundet her; og dette findested i forbindelse med hans andre (nord)sjællandske lokaliteter („Balderup", „Hestangs mølle", „Bognæs") svarer godt til den spredte forekomst af *Hypericum hirsutum*, som AASE KOIE's kort fremviser. *Hypericum pulchrum* (514) angives fra „Højrup"; det er formodentlig det Højrup, der ligger lidt nord for Brahetrolleborg, idet KYLLING har plantefund fra Hillerslev ca. 2 km fra det samme Højrup. De stevnske plantefund plejer han at angive blot ved Stevns. Et evt. *H. pulchrum*-fund ved Højrup i Stevns ville da også falde langt uden for plantens øvrige udbredelsesområde (men kunne måske svare til fundene på Møns Klint), mens Brahetrolleborg-egnen er „kendt" for sine *H.*



*pulchrum*, som det også fremgår af kortet fig. 7. De jyske Højrup'er kan næppe komme i betragtning.

Geraniaceerne (AASE og MOGENS KOIE, 1939) byder ikke på overraskelser hos KYLLING. At *Geranium silvaticum* er fundet „Udi Gyldenlund“ og nu forsvundet, gør WINSTEDT allerede opmærksom på (1925, s. 347); lokaliteten burde derfor være afmærket med en ring på fig. 13.

Araceerne (AASE og MOGENS KOIE, 1939) tæller tre arter, hvoraf de to bør omtales her. *Arum maculatum* har KYLLING fundet på „Magløe“ 5: det nu landfaste Magløe ved Korsør, hvor den ikke er angivet på KOIE'ernes kort fig. 15, og hvorfra den da også nu er forsvundet (eftersøgt forgæves 26.4.54). *Calla palustris* er af KYLLING fundet „Ved Kiøbenhafn, Birkerød, Slagslund etc.“ Mens de to sidste lokaliteter er angivet på kortet og stadig findes, eksisterer København-findestedet naturligt nok ikke mere; det må, i overensstemmelse med KYLLING's sprogbrug, i hvert fald have ligget inden for distrikt 46's grænser og burde her være angivet ved en ring-signatur.

Til AASE og MOGENS KOIE's lemnacé-behandling (1939) er der intet at tilføje fra KYLLING's iagttagelser, og hvad angår droseracé-kortene, der er tegnet af de samme to botanikere, er kun en ring at indføje på fig. 23 inden for København-området.

*Hieracium*-systematik var forstaeligt nok ikke KYLLING's stærke side; WINSTEDT's afhandling fra 1939 kan derfor blive stående uden kyllingsk indblanding.

Noget lignende kan siges om næste punkt: Cyperaceerne er vanskelige at genkende hos KYLLING, og han har kun få af dem. Til WINSTEDT's gennemgang af halvgræsserne (i to omgange: *Scirpoideæ* i 1942, *Caricoideæ* i 1945) kan der derfor kun gøres følgende indvending, der snarere skal rettes mod LINNÉ end mod WINSTEDT. „Det lille slax Ager-Uld, *Gramen tomentosum minus* C. B.” (437) må være *Eriophorum alpinum*, som KYLLING har fundet „Ved Frideriksborg, Assens, oc paa Amager”; på TBU.'s kort er ingen af disse lokaliteter angivet, og de eksisterer ganske sikkert heller ikke mere som voksesteder for Liden Kæruld, men bør indføjes med ring-signaturer; ganske vist har LINNÉ anført BAUHIN's (og KYLLING's) navn til denne plante under *E. vaginatum* og alle KYLLING-forskere har hidtil stolet blindt på den store LINNÉ's opfattelse og regnet med, at KYLLING's lille Ageruld var *E. vaginatum*, og at „Ager-Uld” (436) var *E. angustifolium* (*E. polystachyum*); under dette sidste danske navn har KYLLING imidlertid ganske sikkert begge de to almindelige arter uadskilt, idet han som lat. navn har *Gramen pratense tomentosum panicula sparsa* og synonymet *Linogrostis* (5: *Linagrostis*); disse to navne



plejer ellers at svare til hhv. *E. angustifolium* og *E. vaginatum*. Men især følgende er afgørende: BAUHIN har i sin *Prodromos Theatri botanici* s. 10 en ganske god beskrivelse af *E. alpinum* under navnet *Gramen tomentosum alpinum & minus* (som KYLLING altså blot har forkortet lidt) og s. 23 en endnu bedre beskrivelse af *E. vaginatum* under navnet *Juncus alpinus capitulo lanuginoso* og et billede, der næppe er til at tage fejl af. Vi må altså for *E. alpinum*'s vedkommende regne med de tre gamle, kyllingske lokaliteter, der falder meget naturligt ind i udbredelsesbilledet.

Juncaginaceerne er behandlet af VALDEMAR MIKKELSEN i 1943. På fig. 4 (*Triglochin palustre*) ligger fundene tæt i den sjællandske del af distrikt 46 (København), ligesom næsten hele Danmark er skraveret; kun Amager træder mærkværdigt skarpt og hvidt frem på kortet. Som forholdene er i dag er det fuldt korrekt at vise denne fortrampede ø Kærtrehage-løs (heller ikke i det egentlige København finder vi i dag en eneste *Triglochin*, hvad en uindviet måske kunne vente efter kortet), men på KYLLING's tid fandtes den åbenbart på Amager, idet nr. 444 *Gramen junceum spicatum minus* er denne plante. Amager har jo ikke altid bestået af lossepladser, kålmarker og kolonihaver; men efterhånden som forureningen skred frem, er det klart, at Kærtrehagen måtte vige; under sådanne vilkår kan Strandtrehagen bedre klare sig.

Til *Alismataceæ* (VALD. MIKKELSEN, 1943) hører bl. a. *Sagittaria sagittifolia* (925 og 926), som KYLLING angiver fra flere kendte voksesteder, men desuden fra „Sandby i Seeland“ : Sandby ved Glumsø, hvor voksestedet nok har været Susåen ca. 1½ km fra det egentlige Sandby. Planten eftersøgte her forgæves d. 10. juni i år på en ca. 2 km lang strækning.

Til *Hydrocharitaceæ* er der intet at føje.

Heller ikke om crassulaceerne og saxifragaceerne (MOGENS HOFF, 1943) kan KYLLING berette noget, vi ikke ved.

Derimod må det være tilladt til ALFRED ANDERSEN's behandling af pyrolaceerne (1943) at føje den ingenlunde chokerende oplysning, som KYLLING bringer om *Pyrola minor* (859): „Ved . . . Walloe, Skrydstrup etc.“; også Helsingør nævner KYLLING. Fra omegnen af dette sted foreligger imidlertid herbariebelæg (Hellebæk). Men Vallø og Skrydstrup bør indtegnes med en signatur.

*Plumbaginaceæ* (samme forfatter og år) rummer endnu færre arter. KYLLING har fundet en *Limonium* (587) „Ved Callundborg“, men hvilken af de to hjemlige, hinanden nærstående arter, det drejer sig om, kan selvfølgelig ikke siges. *Limonium* findes næppe mere ved Kalundborg; men efter *L. humile*'s forekomst på det lune Samsø og ved Isefjords og Odense

Fjords bredder, og i betragtning af dens øvrige udbredelse, f. eks. Saltbækvig ikke langt fra Kalundborg, må man vist regne med, at det er denne art, KYLLING har set.

Til campanulaceerne og lobeliaceerne (ALFRED HANSEN, 1948) er intet egentligt nyt at føje. KYLLING har set *Campanula glomerata* (140) „Ved Kiøbenhafns Ladegaard“, der ikke ligger meget fjernt fra Flaskekroen; dette er findestedet for herbarieeksemplaret fra distrikt 46. Begge lokaliteter er nu „forhenværende“. KYLLING's *Campanula rapunculus* (902) fra Frederiksborg stammer måske fra samme indplantning eller såning som den ene eller måske endda begge de herbarieeksemplarer, der er angivet ved to prikker på kortet fig. 8.

Heller ikke til *Orchidaceæ* (JUL. GRONTVED, 1948) er der noget væsentligt at tilføje fra KYLLING; ligesom forrige forfatter har JUL. GRONTVED haft begge KYLLING's kataloger in mente under udarbejdelsen, men næppe studeret dem direkte. Når der således på kortet over *Cephalanthera longifolia* (= *C. ensifolia*) er anført en ring, der refererer til KYLLING's fund i Gyldenlund, så kunne den næsten lige så godt være anbragt på *C. damasonium*-kortet; når M. T. LANGE (1859), som WIINSTEDT (1925) og gennem denne JUL. GRONTVED bygger på, bestemmer KYLLING's *Helleborine montana angustifolia flore albo* til *C. ensifolia*, så beror det på et skøn; de to hvidblomstrede arter blev nemlig ikke adskilt på KYLLING's tid. Men jeg indrømmer gerne, at det er sandsynligst efter de øvrige forekomster af *C. longifolia* og dens førlinnæiske navn at dømme, at det er denne art. Den samme „dobbeltart“ har KYLLING ifølge sin Viridarium set „Ved Walløe“, hvorfra netop både *C. damasonium* og *C. longifolia* kendes og opbevares i Danske Herbarium.

Flere af de behandlede arter figurerer, ligesom det iøvrigt er tilfældet hos de fleste andre topografer, med en bastant forekomst inden for Københavns grænser, belagt med herbarieeksemplar(er). Man får af denne priksignatur det falske indtryk, at arterne stadig findes på lokaliteten, hvad jo næppe kan være tilfældet med *Cephalanthera damasonium*, *Epipactis palustris*, *Gymnadenia conopsea*, *Herminium monorchis*, *Liparis loeselii*, *Listera cordata*, *Orchis morio* og *Orchis ustulata*. Der gøres ofte opmærksom på det korrekte forhold i teksten; men alligevel! Kortenes tavse tale bør ikke give f. eks. udlændinge falske forhåbninger om at kunne svælge i sjældne ordideer og meget andet godt inden for Københavns bygrænse.

På BJARNE EGHOLM's kort over umbellifererne er dette misforhold afhjulpet på den helt rigtige måde. Et kors i cirklen angiver her, at der findes herbariebelæg på forekomsten, men lokaliteten eksisterer ikke mere

som vokseplads for planten; denne praksis er desværre ikke fulgt af de senere topografiske forfattere. Af vore vilde umbelliferer bør følgende tre arter eftersøges på de lokaliteter, KYLLING angiver, *Apium graveolens* (73) „Ved Charise“, *Cnidium dubium* (75) „Paa Saltholmen“. Begge de to planters kyllingske navne er dog lidt usikre, så en ringsignatur er i givet fald ikke påkrævet eller tilrådelig. *Eryngium maritimum* (294) „Ved ... Kiøge, Kiøgekro“. Forekomsten på den sidste lokalitet (= Greve strand) bekræftedes af OSTENFELD i Bot. Tidsskr. bd. 30 (1910) s. 468 og er derfor kommet med på EGHOLM's kort. Endvidere har den forvildede *Levisticum officinale* (582) ifølge KYLLING vokset „ved Drittebro paa denne side Kiøge“ : Driftsbro omtrent, hvor Gl. og Nye Kogelandevej løber sammen. Ialt 21 umbelliferer er forsynet med lokalitetsangivelse(r) hos KYLLING.

Kortene over caprifoliaceerne, adoxaceerne, dipsacaceerne og cucurbitaceerne er tegnet af ALFRED HANSEN (1951). KYLLING har fundet *Dipsacus silvester* (256) „paa Stefnsklint“, hvilken lokalitet bør indføjes på kortet fig. 7 med en ringsignatur; det er usandsynligt, at så iøjnefaldende en plante som Gærde-Kartebolle skulle være overset af vore florister; den må anses for at være forsvundet.

Den sidste af de for 1954 udkomne afhandlinger om karplanternes topografi er K. WIINSTEDT: Pteridofyternes Udbredelse i Danmark (1953). Som allerede antydnet kan det ventes, at KYLLING har f. eks. *Botrychium lunaria* (603) fra lokaliteter, hvorfra den nu er forsvundet på grund af kultivering el. lign. Han skriver således om Alm. Månerude: „Ved Tybjerg, Charise ... Stefnsklint“; disse tre steder kan altså indfojes med en ringsignatur på kortet fig. 7. Også *Ophioglossum vulgatum* (736–39) har KYLLING fundet „Ved Charise“, en lidt afvigende form „Ved gammel Vartou (c: Tuborg), Assens i Fyen“ og en monstrositet „Ved Harslöv udi Seeland“ (c: Haslev); alle disse lokaliteter kan antagelig kun tildeles en ring på fig. 38. *Asplenium ruta-muraria* (924) har som bekendt to klassiske, nu forsvundne voksesteder, Bevtøft og Nustrup kirker, som både KYLLING og WIINSTEDT kender; de er ligesom de andre nu forsvundne steder angivet på kortet ved en ring, selv om der fra flere af lokaliteterne findes herbariebelæg. Denne fremgangsmåde skulle synes bedre end den at bruge udfyldte cirkler i alle de tilfælde, hvor der findes selv nok så gammelt et herbarieeksemplar. På den anden side har vi nu hos vore til dato i alt tolv topografer set tre forskellige signaturer bragt i anvendelse for den slags tilfælde, hvad næppe er holdbart i længden.

Til de øvrige pteridofyter har KYLLING følgende lokaliteter at føje til de allerede kendte: *Blechnum spicant* (597) fundet „Ved Frideriksborg“,

hvorfra den nu sikkert er forsvundet. *Dryopteris thelypteris* (320) også fundet „Ved Frideriksborg“, bekræftet den 8. juni i år; planten står i „Indelukket“ vest for slottet. Hvor vidt en tredje plante fra denne lokalitet kaldet „*Equisetum sylvaticum longissimis setis*, Skov-Hesterrumpe med meget lange borster“ (279) er *Equisetum pratense* er usikkert, om end sandsynligt. Endelig må fundet af *Equisetum telmateia* (273) „Udi Faurdal ved Haderslev“ nævnes; en skriftlig forespørgsel hos en kompetent, lokal mand har endnu ikke givet noget resultat.

Vi er hermed nået igennem de i TBU's publikationsserie for juni 1954 fremkomne afhandlinger. I tilknytning hertil bør måske nævnes C. H. OSTENFELD: Anemone- og Kobjælde-Arternes Udbredelse i Danmark (1911), hvor TBU's materiale er udnyttet. KYLLING har dog ingen „nye“ lokaliteter af større interesse at tilføje, men kun en bekræftelse på det forhold, som C. H. O. gør opmærksom på, nemlig at forekomsten af *Pulsatilla* på Assens-egnen bør underkastes nøjere undersøgelse. De muligvis fejletiketterede herbarieplanter fra Ebberup banker og KYLLING's „*Pulsatilla vulgaris*“ giver os ikke klar besked.

## Summary.

Danish botanical topography and its relation to the *Viridarium* of P. KYLLING.

The earliest, fairly complete list of Danish wild plants is *Viridarium Danicum* (1688) the famous catalogue of P. KYLLING. It comprises 1103 "species" as then conceived, together with information on the localities in which the species are found. Not all the records in KYLLING's list have been included in the papers on the topography of Danish plants, published from 1931 onwards, mostly because the pre-Linnean plant names employed by KYLLING are difficult to interpret, as are many of his locality records.

New detailed information on the identity and locality is here given for a number of KYLLING's species of those families already treated in the topographical survey.

## Litteratur.

- BAUHIN, C., 1671: Pinax Theatri Botanici.  
 — 1671: Prodromos Theatri Botanici.  
 HOLM, G. TYCHO, 1757: Prodromus Florae Danicae.  
 KNUTH, PAUL, 1890: Geschichte der Botanik in Schleswig-Holstein.  
 KYLLING, P., 1684: Gyldenlund.  
 — 1688: Viridarium Danicum.  
 LANGE, M. T., 1859: Om Forandringen af Danmarks Plantevækst.  
 LIND, JENS, 1917: Apoteker C. Heerfordts Herbarier. Bot. Tidskr. 36.

- LINNÉ, C., 1753: *Species Plantarum*.
- OSTENFELDT, C. H., 1911: Anemone- og Kobjælde-Arternes Udbredelse i Danmark. Biol. Arb. tilegn. E. Warming: 241–263.
- SCHLICHTKRULL, O. N. C., 1828: *Quaestio in Historia naturali. De mutationibus vegetationis Daniae* (ms i BBH.).
- WIINSTEDT, K., 1925: Charlottenlund Skov. Bot. Tidsskr. 38.
- TBU: Den topografisk-botaniske undersøgelses protokoller på Botanisk Museum i København.



# The Phylogenetic Position of *Agaricales*

By MORTEN LANGE and LISE HANSEN

## I. On the Occurrence of Clamp Connections of the Medaillon Type in the Fruit Body of some *Agaricaceae*

By LISE HANSEN

Several authors have found specially developed clamp connections occurring in wood-destroying fungi. As will be seen from the figures, these clamp connections—called medallions—differ considerably from the normal type. The clamp is distinctly open, and the side branch and the hypha itself are approximately of the same diameter, often symmetrically developed. (cp. Figs. 1–2, pp. 190–191).

There have been different concepts of the ontology of these medallions. They were first mentioned by FALCK (1909: 148) who thought they were formed through splitting of the hyphae. He found them scattered on the lignicolous mycelium of „*Lenzites*” species, and believed them to be a distinctive generic character. WALEK-CZERNECKA (1933: 286) found medallions in all the wood-destroying fungi studied by her, but she believed they should be regarded as anastomoses formed in three different ways, viz: between two hyphae, between a hypha and its lateral branch, or between two branches of the same hypha. However, ZELLER (1916: 443) had already demonstrated all the different transitions between medallions and normal clamp connections in mycelium of *Gloeophyllum* (*Lenzites*) *sepiarium*, and rightly considered the medallions as modified clamps. Most later authors have accepted this interpretation (e. g. ROBAK, 1942: 84, FARINHA, 1949: 370, HARMSSEN, 1954: 149). Most of these authors found medallions on mycelium in wood, but sometimes also on mycelium on agar or on hyphae in the fruit body.

Medallions have been recorded (or pictured) for the following species of *Homobasidiomycetes*:

- Anisomyces odoratus* (WULF.) PILÁT – ROBÁK, 1942.  
*Dictyopanus luminescens* CORNER – CORNER, 1950.  
*Gloeophyllum abietinum* (BULL.) KARSTEN – FALCK, 1909.  
 – *sepium* (WULF.) KARSTEN – FALCK, 1909, ZELLER, 1916, and others.  
 – *trabeum* (PERS.) MURRILL – FALCK, 1909, CARTWRIGHT, 1932, and others.  
*Lentinus lepideus* FR. – HUBERT, 1924, WALEK-CZERNECKA, 1933, and others.  
*Leptoporus albidus* (FR.) BOURD. et GALZ. – HARMSSEN unpubl.  
 – *borealis* (FR.) PILÁT – HARMSSEN unpubl.  
 – *caesius* (SCHRAED.) QUEL. – HARMSSEN, 1954b.  
 – *fodinarum* (VEL.) PILÁT (= *Poria Vaillantii* PILÁT) – WALEK-CZERNECKA, 1933.  
 – *resupinatus* (BOURD. et GALZ.) PILÁT – WALEK-CZERNECKA, 1933.  
*Merulius molluscus* FR. – HARMSSEN, 1954a.  
*Paxillus panuoides* FR. – FINDLAY, 1932.  
*Trametes betulina* (L.) PILÁT – CARTWRIGHT and FINDLAY, 1946.  
 – *quercina* (L.) PILÁT – WALEK-CZERNECKA, 1933.  
 – *serialis* FR. – CARTWRIGHT, 1930.  
 – *serialis* FR. f. *resupinatus* PILÁT (= *Poria callosa* FR.) – WALEK-CZERNECKA, 1933.  
 – *squalens* KARSTEN – WALEK-CZERNECKA, 1933.  
 – *unicolor* (BULL. ex FR.) COOKE – FARINHA, 1949.  
 – *versicolor* (L. ex FR.) PILÁT – CARTWRIGHT and FINDLAY, 1946.

The list includes 17 species of *Aphylllophorales*, and only three of *Agaricales*. It may be noted, that similar structures are found in several *Tremellales* (*Auricularia auricula*, *A. delicata*, *A. mesenterica*, *A. peltata*, *A. fuscusuccinea* (LOWY, 1952) and *Tremella foliaceae* and *Exidia glandulosa* (MARTIN, 1952).

Working on Greenland species of Agarics, Dr. M. LANGE observed abundant occurrence of medallions in the agaric *Panellus ringens*. In view of the possible taxonomic importance of this observation I was asked to examine a number of Agarics (mainly wood-inhabiting) for the occurrence of medallions on hyphae in the fruit body. The results are listed below:

Medallion clamp connections present.

- Flammulina velutipes* (CURT. ex FR.) SING.  
*Lentinus lepideus* FR.  
 – *ursinus* FR.  
*Panellus mitis* (PERS. ex FR.) SING.  
 – *serotinus* (SCHRAED. ex FR.) KÜHNER  
 – *ringens* (FR.) ROMAGNESI  
 – *stypticus* (BULL. ex FR.) KARST.  
*Paxillus atrotomentosus* FR.  
 – *panuoides* FR.  
*Phyllotopsis nidulans* (PERS. ex FR.) SING.  
*Panus rudis* FR.

Medallion clamp connections not observed.

- Armillaria mellea* (FR.) STAUDE  
*Collybia badia* (LUCAND) J. E. LANGE  
 — *radicata* (FR.) STAUDE  
*Crepidotus mollis* (SCHAEF. ex FR.) QUEL.  
*Hygrophoropsis aurantiaca* (WULF. ex FR.) R. MAIRE  
*Hypholoma fasciculare* (HUDS. ex FR.)  
 — *sublateritium* (FR.) QUEL.  
*Lentinellus bisus* (QUEL. apud BRES.) KÜHNER et MAIRE  
 — *cochleatus* (PERS. ex FR.) KARST.  
 — *vulpinus* (FR.) KÜHNER et MAIRE  
*Lyophyllum ulmarium* (BULL. ex FR.) QUEL.  
*Mycena subalpina* VON HÖHN.  
 — *galericulata* (SCOP. ex FR.) QUEL.  
*Naucoria erinacea* (FR.) GILL.  
*Omphalina sphagnicola* BK.  
*Panus crinitus* (L. ex FR.) SING.  
 — *tigrinus* (BULL. ex FR.) SING.  
*Paxillus involutus* BATSCH  
*Pholiota mutabilis* (SCHAEF. ex FR.) KUMMER  
 — *squarrosa* (PERS. ex FR.) QUEL.  
*Phylloporus rhodoxanthus* (SCHW.) BRES.  
*Pleurotus ostreatus* (JACQ. ex FR.) QUEL.  
 — *dryinus* (PERS. ex FR.) QUEL.  
*Pluteus cervinus* (SCHAEF. ex SECR.) FR.  
*Schizophyllum commune* FR.

The number of medallions varied very much in the different species. They were abundant in all *Panellus* species; in *Panellus ringens* normal clamps could not be found on the trama hyphae; *Paxillus panuoides* had some medallions, but normal clamps were far more frequent; typical medallions were rare in *Paxillus atrotomentosus*, *Lentinus lepideus*, and *Flammulina velutipes*, but several intergrading types were seen. Any type of clamp connections were rare in *Lentinus ursinus*, but some of those seen were typical medallions. In *Panus rudis* well-developed medallions could not be found, but a few clamps came rather near to this type.

Medallions were found both in the stipe and in the cap. They occurred mostly on broad and comparatively thin-walled hyphae, but in *Panellus ringens*, *P. nidulans* and *Lentinus lepideus* they were found also on thick-walled hyphae.

Some of the specimens necessary for the study were kindly provided by Mr. L. HARMSSEN, to whom I offer my best thanks.

## II. Characters Indicating Derivation of some *Agaricales* from *Aphyllophorales*

By MORTEN LANGE.

The conflicting theories on the phylogenetic relations in *Homobasidiomycetes* are not yet ready for synthesis. This small contribution was inspired by the discovery of medallion clamp connections—a supposed “aphyllophoraceous” character—in numerous species of *Agarics*. Its main intention is to bring together some evidence for derivation of *Agaricales* from *Aphyllophorales*, and see how the conclusions affect the other two theories on the derivation of the *Agarics*, viz. either from *Gasteromycetales* or from both *Gasteromycetales* and *Aphyllophorales*. All three possibilities were very ably elucidated by SINGER (1951). His paper should be consulted, as it lists the appurtenet literature published until then.

It seems generally agreed that possible relatives of the *Aphyllophorales* should be sought among *Tricholomataceae* sensu SINGER. The choriaceous species of *Lentinus* s. str. and *Panus* s. str. are probably the most frequently cited (and rightly so), but the genus *Panellus* (as amended by SINGER and by KÜHNER & ROMAGNESI) has also been mentioned. Some characteristic features of *Panellus* seem to me to be of special significance for the whole discussion, because they occur rarely, if at all, in the main groups of *Agaricales* but are common in *Aphyllophorales*.

The allantoid, small spores found in most *Panellus* species deserve special mention. The morphology of the spores generally seems to remain relatively stable throughout the evolution. On this basis it is striking how common the allantoid spore is in *Aphyllophorales* (species of *Corticium*, *Stereum*, *Peniophora*, *Leptoporus*, *Poria*, and many others), while in *Agaricales* such spores are found in but a few genera—all of pleurotoid nature, as far as I know.

Similar importance should be ascribed to the occurrence of medallion clamp connections in all *Panellus* species studied (see above). To this can be added a number of other characters of the genus pointing to a filiation to *Aphyllophorales*: lignicolous habitat, rudimentary stipe (pseudostipe), and a tendency in some species to poroid hymenophore.

Almost all these characters are shared with *Phyllotopsis nidulans*, which is segregated from *Panellus* et al. on account of its nonamyloid, slightly pinkish spores. An inclusion of this species in *Panellus* has much to recommend it. The tropical, poroid *Dictyopanus* seems also very closely

related to *Panellus*. The spores are elliptic like those of *P. stipticus*, and well developed medallions have been illustrated by CORNER (see above).

Another character common to groups of *Aphyllphorales* and to several pleurotaceous fungi is the peculiar cystidia known as metuloids. They are most beautifully developed in *Peniophora*, but they occur in other genera of *Aphyllphorales* such as *Leptoporus*, *Poria*, and *Campnella*. In *Agaricales* they characterize the genera *Geopetalum* and *Hohenbuehelia* sensu SINGER (in the authors opinion the latter genus is not separable from *Resupinatus* sensu SINGER) but they are found also in a few species of *Panus* and *Pleurotus* s. str. Although the chemical reactions of these cystidia vary slightly, the author belives them to be homologous throughout and among other characters indicate a relationship of the *Agarics* in question to *Aphyllphorales*. The pattern of variation in spore morphology inside these *Agaric* genera once more supports this.<sup>1)</sup>

The two features: allantoid spores and metuloids of the *Peniophora* type thus seem restricted to *Aphyllphorales* and pleurotaceous fungi. The third main feature discussed here—the medallion clamp connection—has, however, been found in *Agarics* which are not usually placed in the vicinity of *Pleurotus*, viz. *Flammulina velutipes*, *Paxillus panuoides* and *P. atratomentosus*. *Flammulina velutipes* may, however, find its ultimate place close to some pleurotaceous genus. QUELET even proposed its transfer to *Pleurotus* s. lat. Its binucelate spores and gelatinous cuticle give it a very isolated position in the *Hemimycenae* where SINGER reluctantly placed it; its thick-walled pilocystidia may possibly be atypical metuloids.

But the two *Paxillus* species are true members of their genus (see JOSSEERAND, 1932; ELROD and BLANCHARD, 1939) and more closely related to the *Boletaceae* than to other agaric families. In this view it is very interesting to note, that KÜHNER (1948) has advanced the idea that *Paxillus* should be regarded as a connection between *Boletaceae* and *Aphyllphorales*. This suggestion deserves a careful study. The occurrence of both mycorrhizal and lignicolous species in *Paxillus* is noteworthy in this connection, where a bridge is sought to the almost exclusively mycorrhizal Boleti. The very simple hymenium in *Paxillus* is another important point and the occurrence in two species of medallion clamp connections lends further support to the hypothesis. KÜHNER did not specify the relation of *Paxillus* to *Aphyllphorales* but there are, in fact, quite a few points to suggest a connection between *Paxillus-Boletacea*

<sup>1)</sup> see postscript.



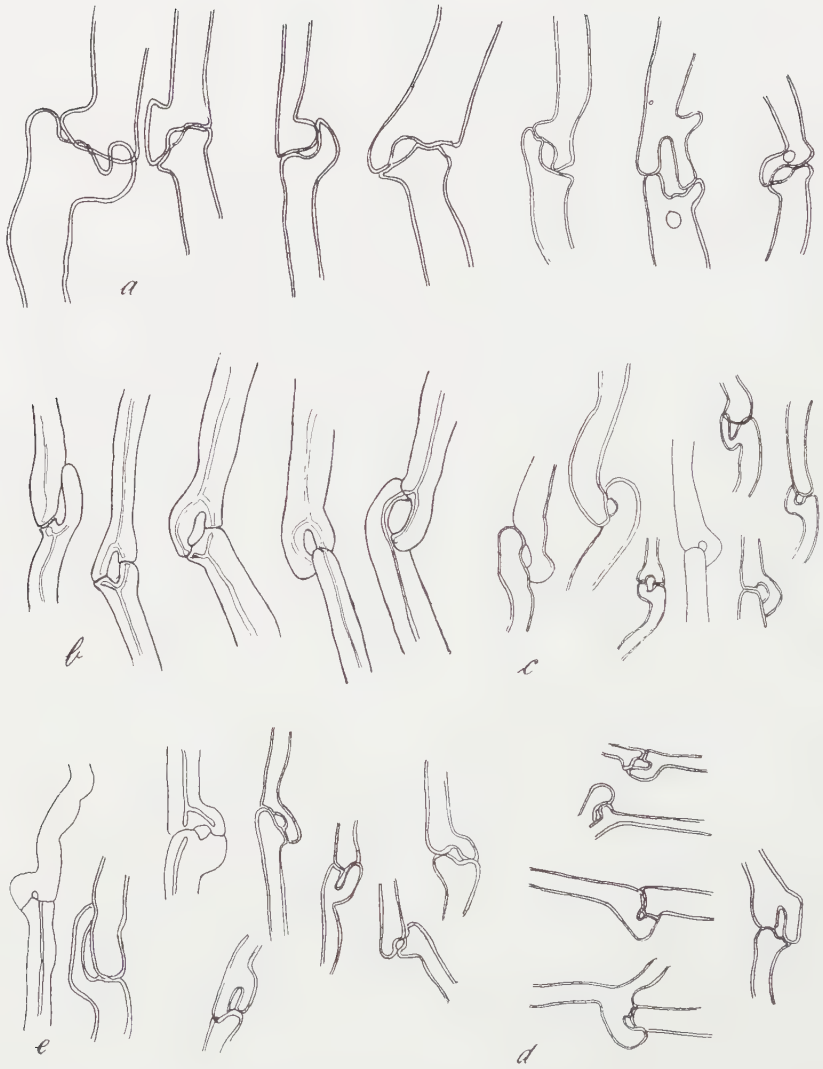


Fig. 1. Medallion clamp connections from the fruit body of a) *Panellus serotinus*, b) *Panellus ringens*, c) *Panellus mitis*, d) *Panellus stypticus*, e) *Phyllostopsis nidulans*.  
 $\times 1000$ .

and the *Meruliaceae*. Most important once again, is the spore characters. The spore colour is almost the same in several *Meruliaceae* and in *Paxillus* and so is the shape of the spores; indeed typical boletoid fusiform spores—rare in most *Holobasidiomycete* families—are found in both *Merulius* and *Coniophora* (viz. *M. fusisporus* ROMELL and *C. fusispora* COOKE &



Fig. 2. Medallion clamp connections from the fruit body of f) *Lentinus ursinus*, g) *Lentinus lepideus*, h) *Panus rudis*, i) *Paxillus panuoides*, j) *Flammulina velutipes*, k) *Polyporellus brumalis*.  $\times 1000$ .

ELL.). The very similar ecology of species of *Coniophora*, *Merulius* and of *Paxillus panuoides* is also worth noting.

There is, of course, a notable hiatus between *Paxillus* and *Merulius* which can hardly be bridged through study of the species of the northern temperate zone, but the gap is not wider than is acceptable when considering problems of phylogenetic relationship, and no more prominent than the hiatus separating the *Boletales* from other groups of *Agarics*.

The characters emphasized above have been chosen for consideration because the author believes that they demonstrate the relation of some Agarics to broad groups of *Aphylllophorales*. SINGER and others have demonstrated affinity between i. a. *Pleurotus* and various polyporaceous fungi, but their evidence has made it necessary to keep the possibility open for a transfer of the Polypores in question to *Agaricales*, and in this way eventually to reach a clear separation between *Aphylllophorales* and *Agaricales*. The occurrence in some *Agaricales* of characters that are widespread in *Aphylllophorales* only permits the opposite classification or the acceptance of a true affinity between the two main groups.

The above-mentioned examples are by no means the only links between *Agaricales* and *Aphylllophorales*. However, the additional examples outlined below have so far been substantiated only by more special characters, and they may represent nothing but reduced series of *Agaricales*, some members of which are now treated in *Aphylllophorales* for traditional reasons. This may be true, for instance, of members of the heterogenous group "*Cyphellinae*", some of which evidently are closely related to such Agaric genera as *Delicatula*, *Marasmius*, and *Galerina* (ROMAGNESI, 1953), and of some species of the "*Laschia*" complex studied by SINGER (1945). I have had no material available for a detailed study of these groups.

The same situations prevails, however, in other groups of whitespored fungi, especially in the *Leptotus-Omphalina* series. A possible relation here was vaguely suggested by SINGER (1951) and also by KÜHNER and ROMAGNESI (1953) who—contrary to SINGER—included *Leptotus* in *Agaricales*. The relation between *Leptotus* spp. and *Omphalina sphagnicola*, *O. epichysium* and their allies is, in my opinion, quite well founded. The spore type is the same in both groups, and it is remarkable that spores in individual species and specimens of these plants have the same pronounced tendency to vary in size and shape. The hymenium is of the same simple type, and the tramal hyphae have identical incrusting pigments. The simple and thin pileus trama of *Leptotus* is no more remarkable than the simple leaf of *Hymenophyllum* among the *Filicinae*—also a highly specialised hygrophyte—and the ecology of *Leptotus* and of the *Omphalina*'s concerned is the same, all of them parasiting mosses.

However, the potential derivation of *Leptotus* from the "*Cyphellinae*" does not prove a definite affinity to true members of *Aphylllophorales* as long as the real position of *Cyphella*, *Solenia* and other genera remains undecided.

A relation between certain *Gasteromycetes* and Agarics is claimed in a growing number of cases; all of the better substantiated examples

includes, however, gasteromycetaceous fungi of the "*Secotiaceae*", *Hydnangiaceae*, and *Hymenogastraceae*. There are, in my opinion, quite good reasons for considering these cases as being analogous to the derivation of certain *Tuberaceae* from epigaeous pezizaceous fungi, i. e. as reduced series. This view-point was strongly and convincingly advocated by HEIM (1952). None of these substantiated relations point towards such important central families as *Phallaceae* (incl. *Hysterangium*), *Nidulariaceae*, *Tulostomataceae*, nor in fact *Lycoperdaceae*, and it is not unlikely that a broad hiatus separates the *Gasteromycetes* proper from the agaricoid groups.

Several authors favour the view that the *Gasteromycetes* should be considered as the ancestral forms in relation to *Agaricales*. The material presented here does not support this point of view. A relation between *Boletaceae* and the Gasteromycete *Rhizopogon* is often claimed, and both morphological and biological evidence for this claim is quite convincing. If the relation *Meruliaceae-Boletaceae* is further substantiated, it would be hard to accept *Merulius* and *Coniophora* as the younger and reduced forms; consequently *Rhizopogon* should be derived from *Boletaceae*, and not vice versa.

If the theory of the Agarics being derived wholly or in part from *Gasteromycetes* is accepted, the logical conclusion is the acceptance of the theory advanced for instance by HOLM (1954), who derives the *Gasteromycetes* from *Tuberaceae*. A detailed study of the spore-morphology, etc. of the two groups gives no material support to this theory. The acceptance of *Aphylophorales* as the ancestral group in *Homobasidiomycetes* will permit a natural bridging to the *Heterobasidiomycetes* through various corticiaceous fungi, and also give a clear relation to some groups of *Agaricales*. It is evident, however, that the position of the central groups in *Agaricales* remains fairly undecided in this system, and indicates an early branching off of these plants—a point which cannot be called astonishing in light of the wide variability encountered in the group.

### Postscript.

The general conclusion advocated above has been further strengthened through our investigations of *Resupinatus applicatus* and *R.rhacodium*. Medallion clamp connections were demonstrated in both. Medallions were further found in two additional species of *Aphylophorales*, viz. *Polyporellus brumalis* and *Cytidia flocculenta*. The latter species shows much affinity to *Resupinatus*.

## Literature.

- CORNER, E. H. J., 1950: Description of two luminous agarics (*Dictyopanus* and *Mycena*). *Mycologia* 42: 421-431.
- CARTWRIGHT, K. ST. G., 1930: Decay of Sitca Spruce timber caused by *Trametes serialis* Fr. A cultural study of the fungus. Dept. Sci. Ind. Res. For. Prod. Bull. 4.
- 1932: Further notes on Basidiomycetes in culture. *Brit. Myc. Soc. Trans.* 16: 304-307.
- CARTWRIGHT, K. ST. G. and FINDLAY, W. P. K., 1938: Principal decay of soft-woods used in Great Britain. H. M. Stationary office, London.
- 1946: Decay of timber and its prevention. H. M. Stationary office, London.
- ELROD, R. P. and BLANCHARD, 1939: Histological studies of the Boletaceae and related genera. *Mycologia* 31: 693-708.
- FALCK, R., 1909: Die Lenzitesfäule des Coniferenholzes. *Hausschwamforschungen* 3.
- FARINHA, M., 1949: Le developpement des anses d'anastomose chez les Hymenomycètes. *Portug. Acta Biol. Ser. A*, 2: 369-371.
- FINDLAY, W. P. K., 1932: A study of *Paxillus panuoides* Fr. and its effect upon wood. *Ann. Appl. Biol.* 19: 331-350.
- HARMSSEN, L., 1954a: De danske *Merulius*-arter. *Bot. Tidssk.* 50: 146-162.
- 1954b: Om *Polyporus caesius* og *Ditiola radicata* som Tømmersvampe. *Bot. Tidssk.* 51: 117-123.
- HEIM, R., 1942: Les voies de l'évolution chez les champignons. *Colloq. Internat. Centre Nat. Recherc. Scient. Évolution et Phylogénie Végétaux*: 27-46. Paris.
- HOLM, L., 1954: Classification et phylogénie des Gasteromycetes. 8 Congr. internat. Bot. Paris 1954. Sect. 19: 54-60.
- HUBERT, 1931: An outline of forest pathology. New York.
- JOSSEERAND, M., 1932: Sur la nature de la trame dans les Genres *Paxillus* et *Phylloporus*. *Bull. Soc. Myc. Fr.* 48: 112-117.
- KÜHNER, R., 1948: Place des Bolets dans l'ensemble des Basidiomycètes et rapports des diverses espèces de Bolets entre elles. *Soc. Nat. Oyonnax Bull.* 2: 37-48.
- KÜHNER, R. et ROMAGNESI, H., 1953: Flore analytique des champignons superieurs. Paris.
- LOWY, B., 1952: The genus *Auricularia*. *Mycologia* 44: 656-692.
- MARTIN, G. W., 1952: Revision of the North Central Tremellales. *State Univ. Iowa. 19. Stud. ser.* 423.
- PILÁT, A., 1936: Atlas des Champignons de l'Europe. 3.
- ROBAK, H., 1942: Cultural studies in some Norwegian wood-destroying fungi. *Medd. 25 Vestlandets forst. Forsøgsstationer.*
- ROMAGNESI, H., 1953: Sur les rapports des Cyphellinées avec certains groupes d'Agaricales. *Proc. 7 Internat. Bot. Congr. Stockholm (1950)*: 407-410.
- SINGER, R., 1945: The *Laschia*-complex (Basidiomycetes). *Lloydia* 8: 170-230.
- 1951: The "Agaricales" (Mushrooms) in modern taxonomy. *Lilloa* 22.
- SNELL, W. H., 1922: Studies of certain fungi of economic importance in the decay of building timbers. *U.S. Dep. Agric. Bull.* 1053: 41 pp.
- WALEK-CZERNECKA, ANNA, 1933: Sur les champignons destructeurs des traverses de chemins de fer en Pologne. *Acta. Soc. Bot. Polon.* 10: 179-290.
- ZELLER, S. M., 1916: Studies in the physiology of the fungi II, *Lenzites saepiaria* Fries, with special references to enzyme activity. *Ann. Miss. Bot. Gard.* 3: 439-509.



## Bornholms botaniske seværdigheder

Af ARNE LARSEN

Noget botanisk jerntæppe forekommer ikke. Vestlige og østlige plantearter vokser fredeligt side om side i Danmarks østligst beliggende provins, klippeoen Bornholm. Arter, der ynder det atlantiske klima med dets kolige og fugtige sommer, efterfulgt af en blid vinter, bliver her sjældne, og deres udbredelsesområder griber ind i forekomstområder for planter, der foretrækker kontinentalt klima med store årlige temperaturudsving og tilbagevendende, tørre tidsperioder.

Adskillige udpræget atlantiske arter findes ikke på Bornholm. Således mangler fuldstændig: Benbræk (*Narthecium ossifragum*), Stor Frytle (*Luzula silvatica*), Engelsk Visse (*Genista anglica*), Klatrende Lærkespore (*Corydalis claviculata*), Småbladet Milturt (*Chrysosplenium oppositifolium*), Rapuntsel (*Phyteuma spicata*), Spæd Mælkurt (*Polygala serpyllifolia*) o. m. a. Flere atlantiske arter har sprunget det øvrige land over og først i de bornholmske klippeområder fundet passende vækstbetingelser. Dette gælder således: Skinnende Storkenæb (*Geranium lucidum*), der mange steder på øen danner tætte bestande, Mur-Gæslingeblomst (*Draba muralis*), der er fundet tre steder på skyggefulde klippeskråninger, og Sort Radeløv (*Asplenium adiantum-nigrum*), hvis glinsende blade dog på Bornholm langt fra opnår den størrelse, der er kendt fra de Britiske Øer, hvor den retteligt hører hjemme. Adskillige atlantiske arter har deres østgrænse på Bornholm: Klokkelyg (*Erica tetralix*) er yderst sjælden og sandsynligvis nu helt forsvundet, Flydende Kogleaks (*Scirpus fluitans*) findes nogle ganske få steder, Smuk Perikon (*Hypericum pulchrum*) ses hist og her i øens centrale skov- og lyngområder; Storblomstret Kodriver (*Primula acaulis*) der i Europa altså ikke forekommer østligere end Bornholm, og forøvrigt heller ikke findes i Sverige, er ret hyppig i de nordbornholmske skove.

Til de udprægede kontinentale arter hører: Bakke-Jordbær (*Fragaria viridis*), Kassubisk Vikke (*Vicia cassubica*) og Svalerod (*Cynan-*

*chum vincetoxicum*), der alle er tem. alm. de fleste steder på øen og ofte ligefrem karakterplanter. Hertil må også regnes en række sjældne arter; således kendes for Bakke-Svovlrod (*Peucedanum oreoselinum*) og Klokke-Vintergrøn (*Pyrola media*) kun nogle få voksesteder, og Bjærg-Kløver (*Trifolium montanum*) er så vidt vides ikke iagttaget i en længere årrække. Melet Kodriver (*Primula farinosa*), der også hører herhen, var for en menneskealder siden t. alm. på enge og endnu o. 1940 farvede den i højsæsonen de sumpede områder ved Bastemose i Almindingen helt røde. Mange steder har denne plante nu fået det for tørt og er gået rivende tilbage eller er helt forsvundet. De smukkeste forekomster ser man i vore dage på strandene mellem Bølshavn og Ypnasted, hvor den endog synes at være i fremgang. Hertil bør føjes nogle i relativ ny tid fra øst indvandrede planter, således Farve-Vajd (*Isatis tinctoria*), der med sine smukke, blågrønne blade og de store hængende skulper, let falder i øjnene, når man møder den på klippekysten, hvor den forekommer hist og her, samt Orientalisk Takkeklap (*Bunias orientalis*), der enkelte steder kan danne store bevoksninger.

En del af de kontinentale arter har deres vestgrænse på Bornholm og findes altså ikke i det øvrige land. Af disse kan nævnes den storblomstrede Sump-Viol (*Viola uliginosa*), der er meget talrig på sit eneste voksested, Vallensgårdsmosen i Åker, hvor den forøvrigt danner alle tænkelige bastarder med almindeligere violarter; hertil hører endvidere Sort Dværgmispel (*Cotoneaster melanocarpa*), der dog ikke er så hyppig som sin nære slægtning og mere atlantisk udbredte Rød Dværgmispel (*C. integerrima*), med hvem den ellers vokser side om side. Den lille Spyd-bladet Skjolddrager (*Scutellaria hastifolia*), der kendes fra strandgrus på strækningen fra Hasle til Hammeren, har også sin vestgrænse her på øen, hvilket ligeledes gælder Bakke Potentil (*Potentilla collina*), der viser lidt af den bornholmske floras slægtskab med Øland og Gotland. Mærkeligt nok er der nogle kontinentale arter, der – omend ret sjældent – forekommer i det øvrige land, men mangler på Bornholm, hvilket f. eks. er tilfældet med Dansk Astragel (*Astragalus danicus*), Blåtoppet Kohvede (*Melampyrum nemorosum*) og Hjortetrod (*Seseli Libanotis*).

Et steds – i dette tilfælde Bornholms – afstand fra Atlanterhavet eller fra det massive kontinent er dog ikke eneafgørende for en plantes optræden. Også stedets solhøjde og daglængde vil være medbestemmende, og dette vil igen sige, at stedets geografiske bredde kan spille afgørende ind. En række nordlige arter har sin sydgrænse på Bornholm; dette gælder således både Selje-Røn (= „Bornholmsk Røn”) (*Sorbus intermedia*) og Finsk Røn (*S. hybrida*), der begge her i landet kun kendes fra

Bornholm. Også Pyramideformet Læbelos (*Ajuga pyramidalis*), Skov-Storkenæb (*Geranium silvaticum*) og en Lovefodart (*Alchemilla filicaulis*) må henregnes til den nordiske gruppe; Engblomme (*Trollius europæus*), der er almindelig mange steder i det øvrige land og udpræget nordisk, mangler på Bornholm.

Af sydlige arter, der forekommer på Bornholm, kan nævnes Kantbælg (*Tetragonolobus siliquosus*), Enblomstret Fladbælg (*Lathyrus sphaericus*), Liden Sneglebælg (*Medicago minima*), Jordbær-Potentil (*Potentilla sterilis*), Strand-Loppeurt (*Pulicaria dysenterica*) og Tarmvrid-Røn (*Sorbus torminalis*), af hvilke den sidste har sin nordgrænse her.

Det er dog næppe Bornholms geografiske beliggenhed, der er den eneste årsag til oens særprægede plantevækst, kort karakteriseret ved sin rige afveksling og adskillige i det øvrige land sjældent forekommende arter. Et væld af muligheder for planter med de mest forskellige livskrav skabes af de stærkt vekslende terrænformer og den stadigt varierende jordbund. Det flade sydland med lerede jorder går over i goldt smeltevandssand, flankeret af klitter i syd; midtlandet med udstrakte klippe- og højlyngsområder, nu for en stor del dækket af skov, slutter af med en nordlig randzone af særdeles fed morænejord og en stejl, forkløftet klippekyst. De mange sprækkedale, der i regelen har et forløb fra nordøst til sydvest, giver rig anledning til dannelse af små vandløb, side engstrækninger eller flade mosedrag; de sydvendte skråninger udtørres i øens særlig regnfattige forsommer og giver derved muligheder for planter, der kræver periodevis udtørring. I klippesidens fugtigere småsprækker skjuler sig bregner og ulvefod, delvis overvoksede med enebær og rose, medens kirsebærtræerne og flere rønnearter hælder udover klippen og om efteråret lyner rødt med blade eller frugter. Selv strandengen mangler ikke, omend det kun drejer sig om mindre pletter, der dukker op på steder, hvor kystklippen træder lidt tilbage og alligevel med sine fremskudte skær yder tilstrækkelig læ for bølgerne; her træffer man store pletter af Kantbælg (*Tetragonolobus siliquosus*), Strandkryb (*Glaux maritima*) og mange andre strandengsplanter.

Det vil være uoverkommeligt at omtale alle Bornholms nævneværdige plantearter, og det følgende udvalg indenfor frøplanter og ganske enkelte sporeplanter må kun betragtes som et forsøg på at fremhæve nogle af de interessanteste, uden skelen til planternes geografiske udbredelsesområder, som omtalt i det foregående, og vi må forestille os, at vi i fællesskab tager nogle ture udover øen.

Nord for Rønne ligger en smuk kulturskov, Sandflugten, der for ca. 150 år siden blev plantet til beskyttelse mod overhåndtagende sand-



Fig. 1. Mose-Vintergrøn (*Pyrola rotundifolia*) træffes t. sj. på sumpede steder i bornholmske skove. Fot. FREDE KJØLLER.

fygning. Skoven er rigt afvekslende med nåletræ-, birke- og egebevoksninger, og i det tynde mosdække har flere sjældne plantearter fundet grobund. Lyserøde, stærkt sodduftende tæpper af Linnæa (*Linnæa borealis*), og alle de syv danske arter af Vintergrøn (*Pyrola*) findes her (fig. 1). Navnlig bør Skærmblofstret Vintergrøn (*Chimaphila umbellata*) fremhæves, da denne i modsætning til de andre arter kun er fundet i denne skov, men heldigvis i mange og livskraftige bestande. Nåleskovsorchideen Knærod (*Goodyera repens*) breder sig flere steder udover mosset og er også i de senere år ved at blive almindelig i plantagerne i nærheden af Dueodde. Iøvrigt må beretningen om de bornholmske orchideer blive et sørgeligt kapitel, idet den overhåndtagende dræning har ødelagt kårene for en række af disse. Dette gælder således Pukkellæbe (*Herminium monorchis*) og Mygblomst (*Liparis loeselii*), der ikke er genfundet de sidste menneske-





Fig. 2. Langakset Trådspore (*Gymnadenia conopsea*) forekommer h. og h. på øens enge. Arten er normalt rødfarvet, men disse to expl. var hvidblomstrede. Fot. FREDE KJØLLER.

aldre, Hvid Trådspore (*Gymnadenia albida*), som i hvert tilfælde nu er yderst sjælden, og Poselæbe (*Coeloglossum viride*), hvis sidst kendte voksested blev ødelagt for en halv snes år siden. Der er dog også indenfor denne familie enkelte lyspunkter; således er Skrueaks (*Spiranthes autumnalis*) (fig. 3) på den kendte og fredede lokalitet i nærheden af Rønne vokset i styrke; Hylde-Gøgeurt (*Orchis sambucinus*) er stadig lige hyppig på nordvestbornholms klippeoverdrev, og der kan da stadig træffes smukke bevoksninger af Salep-Gøgeurt (*O. morio*).

I skovene i Østermarie og enkelte andre steder på øen møder man i forårstiden Bornholms mest særprægede urt, Blegblå Anemone, også kaldet Apennina Anemone (*Anemone apennina* var. *pallida*), der er karakteristisk ved sine talrige blosterblade (fig. 4). Den blev første gang fundet





Fig. 3. Skrueaks (*Spiranthes autumnalis*) blomstrer i september måned. Den er i vore dage kun kendt fra to lokaliteter på øen.

Fot. POUL NØRGÅRD.

i nærheden af Svaneke i året 1866, men da man først havde fået øje for den, viste den sig allerede dengang at være temmelig udbredt. Hvis den, hvad nogle mener, er forvildet fra haver, må denne udvandring være foregået på et så tidligt tidspunkt, at man kvier sig ved at tro, at en så „fin” plante allerede dengang kan have fundet vej til bornholmske bondehaver. Det drejer sig snarere om en virkelig spontan art, og i så fald er den af to grunde meget interessant. For det første er Bornholm det eneste voksested for denne plante nord for Alperne, og den kan være en relikvt – en sidste rest af en tidligere mere udbredt bestand. For det andet har typen hos os i modsætning til den italienske, der er helt blå, bloster-



Fig. 4. Apennina Anemone (*Anemone apennina* var. *pallida*) er navnlig udbredt i skove på den nordøstlige del af Bornholm. Den mangler helt på den sydlige og vestlige del af øen. Fot. FREDE KJØLLER.

blade med helt hvid overside og kun svagt blå underside. Umuligt er det ikke, at den hvide type er en mutant, der er opstået på Bornholm og således stedsen for øen.

Mange af Rø Plantages idylliske vandhuller er fyldt med Dværg-åkanden (*Nuphar pumilum*), den eneste spontane åkande, vi har på Bornholm (fig. 5). Den er i fremgang, og kraftige bevoksninger kan nu bl. a. også ses i nogle af Almindingens moser, hvor planten danner et karakteristisk bælte udenfor rørene.

Akelejen (*Aquilegia vulgaris*) er spontan på Bornholm og skal søges i kratskove i nærheden af Randkløve, men kan også træffes ved Bobbeå og Sandkås; dens blå farve hæver sig smukt i den tætte underskov, og den bærer ikke præg af at være trængt af andre planter. I den mørke, stejlvæggede kløft, Stevelen, ved Rø, hvor Storefos pipler ned over den sorte væg, står den statelige Vedvarende Måneskulpe (*Lunaria rediviva*) i stor mængde, og det er Danmarks eneste naturlige voksested for denne violetblomstrede korsblomst. Op ad kløftens sider lyser gule pletter af Svaleurt (*Chelidonium majus*), der vokser så naturligt og så langt fra beboede steder, at man fristes til at tro, den er spontan. I kløftens bund



Fig. 5. Dværgåkanden (*Nuphar pumilum*) er Bornholms eneste spon-  
tane åkande. I flere af Rø Plantages vandhuller dækker den hele  
overfladen. Fot. FREDE KJØLLER.

mellem Måneskulpe finder man Bredbladet Klokke (*Campanula latifolia*), medens Jordbærpotentil (*Potentilla sterilis*) lader sine ranker løbe udover den smalle sti, og Tandrod (*Dentaria bulbifera*) triller sine små, sorte ynglekopper ned mellem de skarpkantede sten. Denne kløft, der i sin dystre og dog så betagende skønhed byder den botanisk interesserede store oplevelser og vil gøre indtryk på alle, må vi håbe bliver bevaret, skønt tidens krav har ført med sig, at en bro, tilsluttet en fuldt moderne kystvej, det kommende år vil blive lagt hen over dette klippegab!

Paradisbakkerne har ord for at kede børn, men drager til gengæld den voksne naturelsker som en magnet. Næppe noget andet sted på øen træffer man en så frodig vegetation, som i dette områdes mange sprækkedale. Uhyggeligt synes måske nogle det virker, når man begiver sig ud på dalens tykke, bløde *Sphagnum*-puder, når vandet begynder at piple frem, og en forskrækket snog forsvinder ind under nogle store sten, når ledsageren skjules af overdådige Ørnebregner (*Pteridium aquilinum*), og når de tommetykke brombærranker river i læderhuden. Jo vist er man på gyngende grund og ude, hvor sjældent noget menneske færdes, men stemningen drager os videre, og støttende os til de tynde grene af Øret Pil



(*Salix aurita*) når vi da omsider frem til en spændende, lodret klippevæg! Den frostsprængte klippes tynde revner er som skabt til fæste for den næsten græslignende, sjældne bregne, Nordisk Radeløv (*Asplenium septentrionale*), der ikke er bange for den bagende sol, medens dens nære slægtninge, Sort Radeløv (*Asplenium adiantum-nigrum*) og Rundfinnet Radeløv (*A. trichomanes*), foretrækker de mere skyggefulde partier af klippen. Ved klippefoden, delvis voksende ud i mospuderne, står der tuer af Kambregner (*Blechnum spicant*) imellem tæpper af vore to arter Egebregne (*Dryopteris phlegopteris* og *D. linnaeana*), og overalt, både oppe og nede, vrir det med den almindelige Engelsod (*Polypodium vulgare*) og flere Mangelovarter (*Dryopteris*). Længere henne snævrer klostet yderligere ind, og Torstetræ (*Frangula alnus*), Kirsebær (*Cerasus avium*) og højt slyngende, duftende Kaprifolier (*Lonicera periclymenum*) slutter det botaniske vildnis af.

Den klippeknold, hvorpå Hammershus ligger, må regnes for en af de værdifuldeste botaniske lokaliteter i Danmark. Særlig interessant er sydskråningen, hvor solstegete pletter baner vej for tørketålende planter og afløses af skyggefulde klippesprækker med frodig vegetation. Den lille Enblomstrede Fladbælg (*Lathyrus sphaericus*) skjuler sin laksefarvede blomst i det visne græs; blå områder med Aksblomstret Ærenpris (*Veronica spicata*) el. af Smalbladet Klokke (*Campanula persicifolia*) blander sig med gulfarvede partier af Plettet Kongepen (*Hypochaeris maculata*) og får os til at tænke på, at vi ikke er så langt fra Sverige, der kan skimtes i nordvest. Halvvisne småpletter fortæller, at Liden Sneglebælg (*Medicago minima*) allerede er forbi; Løgrodet Rapgræs (*Poa bulbosa*) har spirende småaks, og de mange Knopnelliker (*Tunica prolifera*) udfolder beskedent kun een blomst af gangen. Inde i det lave krat, der delvis består af de tidligere omtalte to arter Dværgmispel, forfølger Svalerod (*Cynanchum vincetoxicum*) botanikeren, og her finder han Kantet Konval (*Polygonatum officinale*), Kassubisk Vikke (*Vicia cassubica*) og enkelte eksemplarer af Ager-Kohvede (*Melampyrum arvense*), medens en kraftig stank af den altødelæggende Ramsløg (*Allium ursinum*), der mange steder på øen optræder som en svobe, trænger op fra bunden af Mølledalen; dog heroppe på den tørre skråning er der ingen fare for, at denne naturens ukrudtsplante skal vinde frem! – Inde i slotsgården optræder Trekloft-Stenbræk (*Saxifraga tridactylites*), ofte på den nøgne klippe, men herinde bærer floraen ellers præg af kulturpåvirkningen, og man finder Kransburre (*Marrubium vulgare*) og Hjertespannd (*Leonurus cardiaca*), der begge på Bornholm, ligesom andre steder i landet er i tilbagegang, samt Tandbæger (*Ballota nigra*), Tornet Tidsel (*Carduus*

*acanthoides*), River (*Asperugo procumbens*) o. m. a. På skråningerne mod vest trækker Kantbælg (*Tetragonolobus siliquosus*) så højt op, som bølgesprojtet når, Bjerg-Perikon (*Hypericum montanum*) iblander sig et væld af Blodrod Storkenæb (*Geranium sanguineum*) og Knoldet Mjødurt (*Filipendula hexapetala*); nede i den gamle voldgravs rørsump kan man være heldig at løbe på Melet Kodriver (*Primula farinosa*), næsten altid sammen med Vibefedt (*Pinguicula vulgaris*), og på den vindblæste skråning ved Tyverenden, oven over den Våde Ovn, forer en bestand af lave puragtige Tarmvrid-Ron (*Sorbus torminalis*) en kummerlig tilværelse.

Lad os da til slut vandre en lille tur ud på øens nordvestlige forpost, Hammerknuden, der ved en sprækkedal er afskåret fra den øvrige ø! „Aldrig har jeg anet, at vi i det egentlige Danmark har et stykke af Grønlands natur!” udbød engang en kender af vor polare landsdel. Ak ja! Det var dengang, da lyngen og andre lave planter var enerådende deruden, og de kuplede vidder kun blev afbrudte af stejle stenvægge. Nu er dette forbi; nåletrær og asp trænger voldsomt på overalt på Bornholm og bør holdes i ave! – På Hammerknuden træffer vi en af de ganske få bornholmske forekomster af Tranebær (*Oxycoccus quadripetalus*); det myldrer her med Hylde-Gøgeurt (*Orchis sambucinus*) og smukke bevoksninger af Kassubisk Vikke (*Vicia cassubica*). Adskillige sjældne karsporeplanter møder man her, således i lyngområderne Flad Ulvefod (*Lycopodium complanatum*), Cypres-Ulvefod (*L. tristachyum*) og Otteradet Ulvefod (*L. selago*). I sumpene er iagttaget Kamillebladet Månerude (*Botrychium matricariifolium*) sammen med Almindelig Månerude (*B. lunaria*) og disses nære slægtning Slangetunge (*Ophioglossum vulgatum*). På klippeskråningen ned mod Hammersø bør botanikeren lede efter Vår-Spergel (*Spergula vernalis*), der desværre ikke er genfundet det sidste årti, og på sletten ved søens nordende vinker en værdig repræsentant for de bornholmske plantesamfund, Den røde Rundbælg (*Anthyllus vulneraria* var. *coccinea*), et farvel og på gensyn til vor interesserede gæst!



# Cytotaxonomical Studies in *Lotus*. I.

## *Lotus corniculatus* L. sens. lat.

By KAI LARSEN

### Introduction.

In the last decade the genus *Lotus* has been studied by several authors from a cytotaxonomical point of view (e. g. GUINOCHET (1946), JALAS (1950) and FAVARGER (1953)). These authors have given special attention to the very polymorphous group *Lotus corniculatus* sens. lat., which will also be the subject of this article.

During a botanical travel to South-West Europe in 1949 supported by the Carlsberg Foundation together with HOLGER S. DAHL and prof. TYGE W. BÖCHER, the author collected a number of seed lots and living plants of the present genus for cytotaxonomical studies and cultivation experiments. This material has been later supplemented by other botanists, and during travels made by the author in Denmark.

The author wishes to express his sincerest thanks to prof. TYGE W. BÖCHER, and to Dr. O. HAGERUP, for their interest in the present investigation, and for their contributions to the experiments in the form of seed lots and transplants from different parts of Europe.

### Cytological and Experimental Results.

#### *Lotus corniculatus* L.

Several authors have stated the chromosome number of this species at  $2n = 24$ . MATTICK (in TISCHLER, 1950), however, found the deviating chromosome number  $2n = 26$  in a plant from Austria, she gives no details about the morphology of this plant, and no drawing of the counted chromosome plate is available. The deviating type found by MATTICK seems, however, to be a local aberrant. In this connection it should be noted that the chromosomes of the genus *Lotus* are relatively small (for

drawings see e. g. GUINOCHET, 1946, FAVARGER, 1953, LARSEN, 1954), and they often stick very close together. The nucleolus has a tendency to disappear very late in the mitotic cycle.

All the cultures, in which the chromosome number has been determined, have also been studied morphologically. *L. corniculatus* has been divided in many varieties and forms, which probably correspond to a number of ecotypes that are difficult to separate morphologically. JALAS (1950) pointed out that the species is an obligate outbreeder, and as the forms occurring in Southern and Central Europe are also frequently cultivated the original population of *Lotus* has received genes from these cultivated forms. JALAS (1950) said that homogeneous populations are found only in the coastal areas of Central and Southern Sweden, in Finland and on Öland and Gottland. In Denmark, too, the inland forms are very much mixed with cultivated races. Most of the Danish material has therefore been collected on coastal slopes and in dune areas.

From the West-Jutland dune areas three cultures (3019, 3020, 3021), which may be referred to var. *crassifolius* PERS., have been cultivated in the Botanical Garden of Copenhagen for four years. In nature this variety is very low-growing with rather small succulent leaves. The succulence has proved to be constant during cultivation, but the experimental plants were much taller and more vigorous than is normal for var. *crassifolius* in nature. No. 645 from North West Jutland may be referred to var. *hirsutus* KOCH (— var. *villosus* THUILL. in LANGE 1886–88); it has been cultivated in the Botanical Garden for several years without changing its characteristic appearance, the small and succulent leaves, the low-growing stature, and the high degree of hairiness. No. 2838 var. *carnosus* HARTM. from the Faroe Islands also remains constant after cultivation for several years. No. 1316 is a southernly coastal type, which must also be referred to var. *crassifolius*; it originates from a steep slope at the Bay of Biscay. It deviates from the Danish representatives of this variety in essential respects; in culture it has preserved its low-growing stature, small leaves and scarce hairiness. Cultivated in the Botanical Garden this strain is rather weak, and every year some plants do not survive the winter. Characteristic too is the very late flowering. Only one plant of No. 1316 had started flowering 25.6.1953. In this connection it can be mentioned that No. 3021 from West Jutland, flowering earliest of all the strains investigated, started to flower 20.5.1953. The other West Jutlandish strains and var. *carnosus* from the Faroe Islands too were early flowering.

The Central-European inland forms show a greater variability than the coastal forms. A nearly glabrous, large-leaved and very vigorous type is represented by Nos. 1848, 1953, 2015, and 2032; these cultures can be referred to var. *arvensis* SER. f. *silvaticus* KOCH. This form was previously regarded as a modification, but the cultivation experiments have revealed that it keeps constant during cultivation. It is possible, however, to find transition forms between f. *silvaticus*, which is glabrous, and f. *ciliatus* KOCH which is very hairy.

The size of the leaves in var. *arvensis* also proved to be genetically determined.

*Lotus corniculatus* L. var. *alpinus* SER.

(Syn.: *L. glareosus* BOISS. & REUT. var. *glacialis* BOISS. & REUT., *L. alpinus* SCHLEICH., *L. glacialis* BOURG., *L. corn.* var. *L. alpinus* BECK).

This variety deviates in being diploid (FAVARGER, 1953, LARSEN, 1954). ASCHERSON & GRAEBNER (1906-10) transplanted some presumptive cultures of var. *alpinus* from the Alps to the Botanical Garden of Berlin. Some of these cultures remained typical var. *alpinus*, while others developed into vigorous forms of *L. corn.* Unfortunately the chromosome numbers of these cultures were not counted. FAVARGER (1953) also mentions some plants which BECHERER had referred to var. *alpinus* but which, in a cytological examination, were found to have  $2n = 24$ .

No. 1805 was sown in the Botanical Garden of Copenhagen in 1950; its characteristic appearance did not alter in the two years during which it was cultivated. It died in 1952 after a very luxuriant flowering in the previous summer.

Some of the characters of var. *alpinus*, e. g. the small seeds and pods, may be referred to the diploid status of the former. Unfortunately No. 1805 died before the cell size, the pollen, the stomata, and other characters of importance in chromosome races could be studied. However, it is interesting to note that the flowers of var. *alpinus* are bigger than those of typical *L. corn.*, although it should be born in mind that very large-flowered tetraploid types occur such as var. *carnosus*.

The geographic distribution of var. *alpinus* is rather wide; it occurs in high mountains in Europe in the Iberian peninsula, (e. g. Sierra Nevada), the Pyrenees, the Alps, the Balcan peninsula; it is also found in North Africa, and in Western Asia as far as the Himalayas, but we have no certain knowledge of the range of the diploid.

*Lotus tenuis* WALDST. & KIT.

In the Scandinavian botanical literature this type is generally considered a separate species, while Central and Southern European florists usually classify it as a subspecies or a variety of *L. corniculatus*. This may be due to the wider range of variation of *L. tenuis* with transitional forms to *L. corn.* in Central and even more so in Southern Europe. Culture No. 3022 from Fanø preserved its typical appearance in cultivation; this is in accordance with earlier experiences (ASCHERSON & GRAEBNER, 1906-10).

This species is diploid, having  $2n = 12$ . This, in conjunction with ecological and morphological data make it justifiable to regard it as a separate species, in any case in Northern Europe.

*Lotus uliginosus* SCHKUHR.

The Danish material of this species may be divided morphologically into two types.

Var. *glabriusculus* BABINGT. is a glabrous or nearly glabrous form with 4-10 flowers in the inflorescence. The flowers are rather large and light yellow.  $2n = 12$ . By far the most common form.

Var. *villosus* LAMOTTE (Syn.: *L. ulig.* var. *vestitus* LGE., *L. pilosus* BEEKE). This variety is abundantly hairy; the inflorescence has 8-14 flowers, which are smaller than those of var. *glabriusculus*. and have a darker yellow colour.  $2n = 12$ .

LANGE (1886-88) mentioned var. *villosus* which, incidentally, is missing in new Danish floras. Its distribution was treated by JESSEN (1931). It comprises two ecological races: one which prefers dry habitats (represented by No. 3126 originating from a dry slope on Jersey), and one which, like var. *glabriusculus* grows in humid habitats. It is the latter race that occurs in Denmark where it is represented on the islands Fanø, Manø and Rømø. On these islands it is found in humid depressions and along ditches. It has also been found in a couple of similar localities in West Jutland. Var. *villosus* seems to be most frequent in the atlantic Western Europa, but it has also been found near Vienna.

MILOVIDOV (1941) counted  $2n = 24$  in material from the Botanical Garden of Göttingen; only further studies can reveal whether *L. uliginosus* comprises two polyploids.

*L. uliginosus* is a well-defined species in North and Central Europe, but in Southern Europe its delimitation against *L. corniculatus* is often difficult and by several authors it has been regarded as a variety of *L. corn.*

### Discussion and Conclusions.

(1). In *Lotus corniculatus* sens. lat. three diploid types, *L. corn.* var. *alpinus*, *L. tenuis* and *L. uliginosus*, and one tetraploid type *L. corniculatus* sens. str. are included. The tetraploid type has the largest distribution, which corresponds to the majority of known distributions of diploids and tetraploids. *Lotus uliginosus*, however, has nearly the same distribution area as *L. corn.*; *L. corn.* var. *alpinus*, a diploid type, is found, at high altitudes in the alpes. This does not agree with the general conclusions of the HAGERUP-TISCHLER theory.

(2). The three species of the genus *Lotus* occurring in Denmark, *L. tenuis*, *L. uliginosus* and *L. corniculatus* are not difficult to distinguish in North Europe, but in Southern, and especially in South-Eastern Europe, these species have so wide variations that according to the floristic manuals it is often extremely difficult to keep them apart. The author has not yet been able to cultivate *Lotus* from these areas, but as obligate outbreeders, we may have to face the problem of frequent intercrossing, and the great variability may be due to the formation of hybrid swarms between *L. uliginosus*, *L. tenuis* and, maybe, diploid *L. corn.* races.

(3). The phylogenetic relationship in the *L. corniculatus*-group has been dealt with by several authors (DAWSON, 1941; TOME & JOHNSON, 1945; GUINOCHET, 1946; FAVARGER, 1953). It seems clear that *L. corn.* is derived from polyploidy; *L. tenuis* has often been indicated as the diploid species from which *L. corn.* developed through autotetraploidy. However, artificially produced autotetraploid *L. tenuis* (TOME & JOHNSON, 1945) does not resemble *L. corn.*; nor has it been possible to obtain viable seeds from the crosses between *L. corn.* and autotetraploid *L. tenuis*. Another possibility, however, has appeared with the discovery of the diploid *L. corn.* var. *alpinus*. This type could well be the ancestor of the tetraploid species. Studies by DAWSON (1941) in which tetrasomic inheritance was demonstrated, and the fact that var. *alpinus* and *L. corn.* resemble each other more closely than any of the other species of the *Lotus corniculatus*-group suggest that the latter species was derived through autopolyploidy from var. *alpinus*. The possibility that *L. corn.* may have arisen by amphidiploidy cannot be disregarded, however.



Table showing cultures, for which the chromosome numbers have been determined.

(O.H.: O. HAGERUP, T.W.B.: TYGE W. BÖCHER, T.C.: TYGE CHRISTENSEN. \*: seed samples from wild sources obtained through botanical gardens).

	Culture No.	Locality
<i>Lotus corniculatus</i> L. var. <i>hirsutus</i> KOCH. ....	645	Denmark: Stenbjerg, North-West Jutland; coll. T.W.B.
var. <i>sativus</i> HYL. ....	2204	— Hillerød, North Zealand, gravel slope.
var. <i>carneus</i> HARTM. ....	2838	— The Faroe Islands; coll. O.H.
var. <i>crassifolius</i> (PERS.) SER. ....	3018	— Skanshage, North Zealand; coll. T.W.B.
var. <i>crassifolius</i> ....	3019	— Rømø, in the dunes.
var. <i>crassifolius</i> ....	3020	— Fanø, in the dunes.
var. <i>crassifolius</i> ....	3021	— Hvide Sande, West Jutland, in the dunes.
var. <i>crassifolius</i> ....	3145	Ireland: Newcastle, at the beach; coll. T.W.B.
var. <i>arvensis</i> SER. f. <i>genuinus</i> POSP. ....	1316	France: St. Jean de Luz, rocky slope.
var. <i>arvensis</i> f. <i>genuinus</i> ....	1523	— Gavarnie, in the Pyrenees. 1500 m. above sea level.
var. <i>arvensis</i> f. <i>genuinus</i> ....	2409	Germany: Frankfurt a. M. *
var. <i>arvensis</i> f. <i>genuinus</i> ....	1349	Spain: Miñao, near Bilbao.
var. <i>arvensis</i> f. <i>genuinus</i> ....	1373	— Peña Bargindia, South of Bilbao. 400 m. ab. s. l.
var. <i>arvensis</i> f. <i>genuinus</i> ....	1921	Switzerland: Kleine Scheidegg, Interlaken. 2000 m. ab. s. l.
var. <i>arvensis</i> f. <i>rubriflorus</i> LAMOTTE ....	1571	France: Plateau de Paila (Gavarnie), in the Pyrenees. 2200 m. ab. s. l.
var. <i>arvensis</i> f. <i>silvaticus</i> BAUMG. ....	2015	— North of Court (Jura).
var. <i>arvensis</i> f. <i>silvaticus</i> ....	2032	— Bussang (Voges).
var. <i>arvensis</i> f. <i>silvaticus</i> ....	1848	Switzerland: Le Sepay, meadow. 1000 m. ab. s. l.
var. <i>arvensis</i> f. <i>silvaticus</i> ....	1953	— Schynige Platte, Interlaken. 2000 m. ab. s. l.
var. <i>arvensis</i> f. <i>ciliatus</i> KOCH (pro var.) ....	1665	France: Formigueres, in the Pyrenees. 1600 m. ab. s. l.
var. <i>arvensis</i> f. <i>ciliatus</i> ....	1839	— Mont Salève at Geneva. 900 m. ab. s. l.
var. <i>arvensis</i> f. <i>ciliatus</i> ....	1877	Switzerland: Col de Pillon. 1700 m. ab. s. l.
var. <i>arvensis</i> ....	2189	— Brienzler Rothorn. 2100 m. ab. s. l.
var. ? ....	2436	Yugo-Slavia: Zagreb. *
<i>Lotus corniculatus</i> L. var. <i>alpinus</i> SER. ....	1805	France: Glacier Bionnassay at Mont Blanc. 2800 m. ab. s. l.
<i>Lotus tenuis</i> WALDST. & KIT. ....	3022	Denmark: Sønderho. Fanø, Salt marsh.
<i>Lotus uliginosus</i> SCHKUHR. var. <i>villosus</i> LAMOTTE. ....	3126	Jersey; coll. T.W.B.
var. <i>glabriusculus</i> ....		Denmark: The Botanical Gardens in Copenhagen.
var. <i>glabriusculus</i> ....	3561	— Springbog, west of Legind, Mors, North Jutland; coll. T.C.
var. <i>glabriusculus</i> ....	3562	— Bog north of Højris castle, Mors, North Jutland; coll. T.C.

## Literature.

- ASCHERSON, P. & GRAEBNER, P., 1906–10: Synopsis der mitteleuropäischen Flora. VI, 2. – Leipzig.
- BÖCHER, T. W., LARSEN, K. & RAHN, K., 1953: Experimental and cytological studies on plant species. I. *Kohlrauschia prolifera* and *Plantago coronopus*. – *Hereditas* 39.
- BRAND, A., 1898: Monographi der Gattung *Lotus*. – *Engl. Bot. Jahrb.* 25.
- DAWSON, C. D. R., 1941: Tetrasomic inheritance in *Lotus corniculatus* L. – *Journ. of Genet.* 42.
- FAVARGER, C., 1953: Note de caryologie alpine. II. – *Bull. Soc. Neuchatel. Sci. Nat.* 76.
- GUINOCHET, M., 1946: Recherches de taxonomie expérimentale sur la flore des Alpes et de la région méditerranéenne occidentale. III. Note caryosystématiques sur le *Lotus corniculatus* L. sens. lat. – *Rev. de Cyt. et de Cytophys. Veg.* 8.
- JALAS, J., 1950: Zur Kausalanalyse der Verbreitung einiger nordischen Os- und Sandpflanzen. – *Ann. Bot. Soc. Zool. Bot. Fenn.* "Vanamo" 24.
- JESSEN, K., 1931: The distribution within Denmark of the higher plants II. The distribution of Papilionaceae within Denmark. – *Kgl. dan. Vidensk. Selsk. Skr. nat. mat. Afd. 9. Række. III.* 2.
- KAWAKAMI, J., 1930: Chromosome numbers in Leguminosae. – *Bot. Mag. Tokyo* 44.
- LARSEN, K., 1954: Chromosome numbers of some European flowering plants. – *Bot. Tidsskr.* 50.
- LANGE, JOH., 1886–88: Haandbog i den danske Flora. – København.
- LÖVE, A., 1948: Chromosome numbers of northern plant species. – Reykjavík.
- MILOVIDOV, P. F., 1941: Über die Chromosomenzahlen bei einigen Leguminosen und andere Pflanzen. – *Planta* 32.
- SENN, H. A., 1938: Chromosome numbers in the Leguminosae. – *Bibliograph. Genet.* 12.
- TARNAVSCHI, J. T., 1947: Die Chromosomenzahlen der Anthophyten-Flora von Rumänien mit einen Ausblick auf das Polyploidie-Problem. – *Bul. Grad. Bot. Muz. Bot. Univ. Cluj.* 28. Suppl. 1.
- TISCHLER, G., 1950: Die Chromosomenzahlen der Gefässpflanzen Mitteleuropas. – s'Gravenhage.
- TOME, G. A. & JOHNSON, I. J., 1945: Self- and cross-fertility relationships in *Lotus corniculatus* L. and *Lotus tenuis* Waldst. et Kit. – *Journ. Amer. Soc. Agronom.* 37.

## Notes on *Cercidiphyllum magnificum* NAKAI

By BERTIL LINDQUIST

*Cercidiphyllum japonicum* was described by SIEBOLD and ZUCCARINI (1846). It lasted more than 60 years before we got the first note of a more outstanding variety of it, given by REHDER & WILSON (SARGENT, 1913, p. 316), who mentioned var. *sinense* from relative high altitudes in the Chinese provinces Shensi, Szetchuan, and Hupeh. The new variety was given a rather vague description—the authors had not been able to examine flowers and fruits—with emphasis on stem type and on the leaves, which are pronouncedly cordate and have a slight pilosity on the veins underneath. The authors were of the opinion that “it would appear best to consider it as a variety distinct from the Japanese type”. This variety was rapidly introduced into American and English gardens.

Six years later NAKAI (1919, p. 299) gave a brief description of another variety of *Cercidiphyllum japonicum* which he called var. *magnificum*. It was characterized by bigger and more rotundate leaves which at their base were pronouncedly cordate. His description, which was made in Japanese only, runs as follows: “The longitudinal furrows of the stem of *C. japonicum* begins at a diameter of the trunk of 6–10 cm., but in the new variety first when the trunk reaches about 20 cm. The leaves are broader and more rugose.—Japanese name: Broad leafed Katsura. Found on Mt. Maeshirane and in Konsei Toge 8.9.1919.”

The year after (1920, p. 35) he made his new variety a species, *Cercidiphyllum magnificum*. The new contribution was published in a seed list from Tokyo Botanical Garden. It follows here: “Differt a *C. japonico*, truncis divaricatis cortice tarde fisso, foliis latioribus rugosis, petiolis viridibus, seminibus albescentibus utrinque alato-attenuatis.

Usque 20 metralis altus. Cortex trunci cinereus circiter 20 cm. latus longitudine findere incipit. Ramus elongatus glaber lenticellis punctuatus, brevis vermicularis. Petioli 1,5–3 cm. longi 1–2 mm. crassi virides.



Fig. 1. *Cercidiphyllum magnificum*. Specimen from Gothenburg Botanic Garden. Note the strongly developed dwarf-shoots.

Folia rotundata palmatinervia margine crenata supra venis impressis rugosa viridia, infra pallida venis eleatis. Flos breve pedicellatus. Perigonii segmenta purpurascens integra v. erosa. Stamina numerosa pendula antheris apice apiculatis. Pedicelli fructiferi 3-5 mm. longi. Follicula 13-17 mm. longa in stylum attenuata. Semina albescentia utrinque alata."

As far as I know, *Cercidiphyllum magnificum* has, curiously enough, been totally ignored in both European and American scientific literature,





Fig. 2. Extremely developed long shoots of *C. magnificentum* (left) and *C. japonicum* (right).

and no detailed investigation as to its taxonomical value and its relation to *C. japonicum* and its var. *sinense* seems to have been published.

The Japanese botanists who after NAKAI have dealt with this genus have all followed NAKAI's concept of 1920 and treated his new unit as a species (INOKUMA, 1931, MAKINO, 1951, OHWI, 1953). INOKUMA follows NAKAI's description and illustrates excellently the differences in bark type





Fig. 3. Seeds of *C. magnificum* (left) and *C. japonicum* (right). In *C. magnificum* the seed is slightly visible in the centre between the two seed wings, in *C. japonicum* the seed can be seen in upper end with the wing below. The seeds are here placed with their distal ends up.

between the two species. OHWI also gives a detailed diagnosis in Japanese: "Seed winged on both ends. Bark not splitted when young. Leaves slightly larger, those on a short branch almost round, rounded at the apex, usually deeply cordate at the base, those on a long branch usually obtuse at the apex".

This new species is not recorded in RHEDER's recent "Bibliography of cultivated trees and shrubs" (1949) nor in the second edition of his "Manual" (REHDER, 1949) although *C. japonicum* var. *sinense* is mentioned in the latter with a fairly brief diagnosis. SCHENCK (1939) gives very accurate data on *Cercidiphyllum japonicum* but does not mention *C. magnificum*. Still there are interesting details in his book from the region of Japan where *C. magnificum* seems to be quite common and *C. japonicum* rare. He mentions *C. japonicum* var. *sinense* in about the same words as did RHEDER & WILSON.

The same lack of information is found in ASCHERSON & GRAEBNER (1929), JENSEN et al. (1948), and KRÜSSMAN (1951). In the "Mitteilungen der deutschen dendrologischen Gesellschaft" I have been unable to find information about this tree.

I had the opportunity to study *Cercidiphyllum japonicum* and *C. magnificum* in the field during my journey in Japan in 1952 and also in the

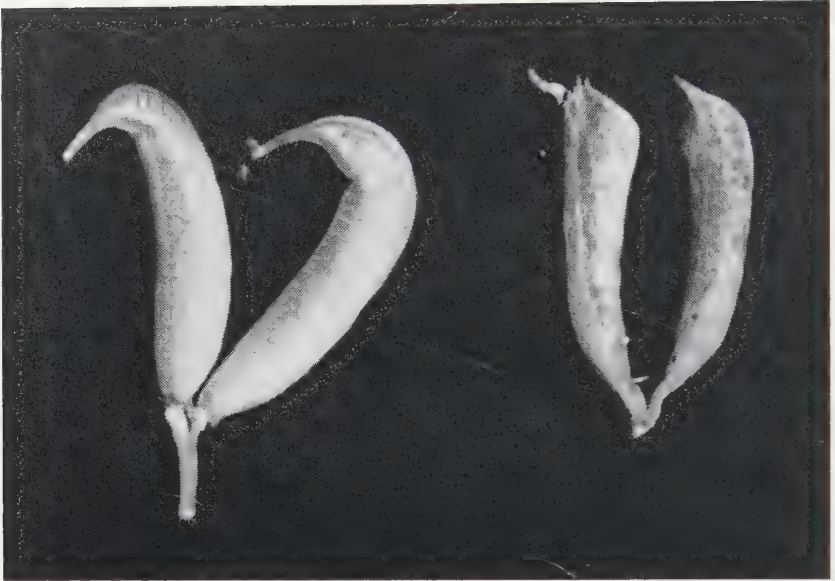


Fig. 4. Follicles of *C. magnificum* (left) and *C. japonicum* (right). The style is longer in *C. magnificum* and the top of the follicles is strongly incurved.

Botanic Garden in Göteborg, where both have flowered the last five years. They seem to show very distinct differences.

In all examined localities the stem form of the young trees show the same significant differences as NAKAI states and INOKUMA (l. c.) so nicely has illustrated, with smoother bark in *C. magnificum* and more strongly furrowed bark in *C. japonicum*. From what I have seen of *C. japonicum* it is quite a big tree with a straight or, more often, a little slanting stem. It competes on good soils with success with species of *Abies* and *Picea* and with *Tilia japonica*, *Quercus grosseserrata* and *Kalopanax pictum* in the highest forest layer in the north of Japan (MIYABE & KUDO, 1925-28, p. 26). As far as I have seen *C. magnificum* very seldom attains bigger dimensions. It is a small, slanting one stemmed tree in the lower forest layer together with *Prunus Grayiana*, *Acer japonicum*, *A. Shirasawanum* and others.

There are also some marked differences in the development of the dwarf-shoots, which are strongly developed in *Cercidiphyllum magnificum* but are nearly lacking in *C. japonicum*.

In *C. magnificum* the leaves are strongly cordate with overlapping lobes on the dwarf shoot leaves, while those of *C. japonicum* are only slightly cordate. The petioles of *C. magnificum* show an obtuse angle with the



Fig. 5. The distribution of *Cercidiphyllum magnificum* according to reports from NAKAI (1920), INOKUMA (1931) and to herbarium specimens (Göteborg, Stockholm, Tokyo).

midrib of the leaves, but in the leaves of *C. japonicum* there is a more right angle between blade and petiole.

The serration of the leaves is coarser in *C. magnificum* than in *C. japonicum*.

Some Japanese authors have pointed out that the leaves of *C. japonicum* are quite glabrous, differing in this respects from the leaves of *C. magnificum* which are said to be pilose on the basis of the veins underneath. I have been able to confirm that some few individuals in the populations of *C. magnificum* show a slight pilosity, but most of them are glabrous.

All young plants of *C. magnificum* in the nurseries in Göteborg were glabrous. All specimens of *C. japonicum* which I have inspected were glabrous.

It is quite obvious that the follicles of *C. magnificum* are thicker and longer and more arcuate at the apex than those of *C. japonicum*, with a longer part of the style persisting. Other important differences are to be found in the shape and development of the seeds. The colour of the seed of *C. japonicum* is medium brown, in *C. magnificum* yellowish white. As NAKAI and OHWI states, there is only one seed wing in *C. japonicum*, but two in *C. magnificum*. In *C. japonicum* there is a proximal wing with the seed at the apex, in *C. magnificum* a proximal wing and a smaller distal one with the seed in between. The proximal wing is more acute in *C. magnificum* and shows two well marked veins in its reticulate structure which converges at the apex (Fig. 3). In *C. magnificum* the thickened ridges of the seed are still more prominent than in *C. japonicum* and they are sometimes wing-like.

The differences between *C. magnificum* and *C. japonicum* given here make it apparent that these species must be considered well established. In localities in Japan where they both occurred together I have not been able to discover any intermediate forms nor have any intermediates been found in the thousands of seedlings (cultivated in the Botanic Garden in Gothenburg) which I have examined. Although the mother trees grow close to each other in the Garden.

*C. magnificum* seems to have a narrow distribution area, concentrated to the Japanese alps and the Nikko region, corresponding with the distributions of certain conifers, e. g. *Larix leptolepis* and *Abies Veichii*. There is an isolated locality in the Province of Iwate in northern Honshu, in Mount Hayashine, which from a plant geographical point of view shows many interesting features.

*C. japonicum*, on the other side, is a very common tree in the forests of middle and southern Hokkaido and in northern Honshu. It is scattered throughout Central and South Japan. In Nagano and Tochigi Prefectures, where *C. magnificum* is more common, *C. japonicum* is often rare.

The relationship between *C. japonicum* var. *sinense* REHD. & WILS. and *C. magnificum* seems never to have been discussed in the botanical literature. As I have previously mentioned the descriptions of var. *sinense* are vague, both the diagnosis and the comments by later authors (cfr. LEE, 1935). And HARMS (1917), who investigated the genus *Cercidiphyllum* thoroughly, has expressed his sincere doubts as to this variety. It is necessary to make a reinvestigation of this variety in the light of the new

viewpoints. Very much points against a closer relationship between *C. magnificum* and *C. japonicum* var. *sinense* than between var. *sinense* and its main species.

I have found it worth while to throw light upon NAKAI's ignored species. This seems to be important not only from the taxonomic point of view but also from a horticultural one. *C. magnificum* seems to belong to the elite of exotics fit for Central and Northwestern European gardens.

### Literature.

- ASCHERSON & GRAEBNER, 1929: Synopsis der Mitteleuropäischen Flora V (2). – Leipzig.
- HARMS, H., 1917: Zur Kenntnis der Gattung *Cercidiphyllum*. – Mitteil. Deutsch Dendrol. Ges. 26. – Thyrow.
- INOKUMA, T., 1931: Preliminary notes on the ligneous plants indigenous in the "Chichibu" University forest and its adjacent districts. – Bull. Tokyo Imp. Univ. Forests, 14. – Tokyo.
- JENSEN, V., PALUDAN, H. K. & SÖRENSEN, C. TH., 1948: Buske og Træer. – København.
- KRÜSSMANN, G., 1951: Die Laubgehölze. – Berlin.
- LEE, SHUN-CHING, 1935: Forest Botany of China. – Shanghai.
- MAKINO, T., 1952: An Illustrated Flora of Japan (in Japanese). – Tokyo.
- MIYABE, K. & KUDO, Y., 1925–28: Icones of the essential forest trees of Hokkaido. – Sapporo.
- NAKAI, T., 1919: A New Variety of *Cercidiphyllum japonicum* (T. Nakai) (in Japanese). – Bot. Mag. 33. Tokyo.
- 1920: Catalogus seminum et sporarum Hortus Botanicus Universitatis Imperialis Tokyoensis. – Tokyo.
- OHWI, J., 1953: Flora of Japan (in Japanese). – Tokyo.
- REHDER, A., 1949: Manual of cultivated trees and shrubs. 2nd ed. – New York.
- 1949: Bibliography of Cultivated Trees and Shrubs. – Jamaica Plain, Mass.
- REHDER, C. & WILSON, C., 1913 in SARGENT: Ch.: Plantae Wilsonianae Vol.(1. – Cambridge.
- SCHENCK, C. A., 1939: Fremdländische Wald- & Parkbäume, 3. – Berlin.



## Notes on Some *Hypocreales* Recently Found in Denmark

By ANDERS MUNK

In current literature the typical *Ascomycetes* *Pyrenomycetes* are distributed upon *Hypocreales* (with a hyaline or coloured perithecial wall), *Sphaeriales* (with a black perithecial wall), and *Dothideales* (perithecia without individual walls). The largest group, *Sphaeriales*, has appeared to be highly heterogeneous (cp. e. g. MUNK, 1953). *Dothideales* (cp. MÜLLER & v. ARX, 1950; LUTTRELL, 1951) seems to be a natural group after exclusion of certain genera, e. g. *Phyllachora*. The situation in the taxonomy of *Hypocreales* is rather curious. Intensive studies have been made concerning the delimitation of species within the group, especially in the genus *Nectria*, and many very difficult problems have been elaborately solved (cp. e. g. the papers of SEAVER, WOLLENWEBER, and, especially, WEESE). But we know very little concerning the morphology of these fungi; consequently, the well-finished picture of the taxonomy on the level of species is combined with an almost total lack of taxonomy on higher levels.

The genus *Nectria* was previously discussed by the author (MUNK, 1954b), and the whole *Hypocreales*-problem will be discussed in a future paper (MUNK, 1954c). The present paper gives an account of noteworthy *Hypocreales* recently found in Denmark.

### *Barya parasitica* FCK.

On decaying *Bertia moriformis* (TODE ex FR.) DE NOT. (soc. *Ophionectria cerea* (BERK. & CURT.) SEAVER, see below) on a decorticated branch of *Fagus silvatica*. – Silkeborg Vesterskov 29. viii. 1953.

This fungus seems to be very rare as is the other Danish species of the genus: *B. lichenophila* FERD. & WINGE; it is a question whether it has

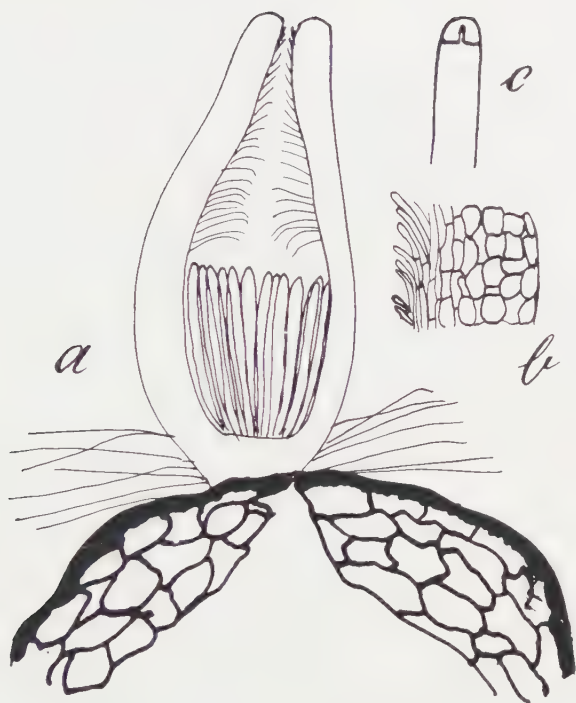


Fig. 1. *Barya parasitica* Fck. — a) Section (half-schematic) through a perithecium on *Bertia moriformis*,  $\times 130$ . — b) Detail of the peridium,  $\times 300$ . — c) Ascus-top,  $\times 1500$ .

been found anywhere since the time of FÜCKEL. The Danish material is very beautifully developed; a description will be given here:

Mycelium white, producing a tuft on the top of the host or expanding over larger areas when the perithecia of the host are densely crowded. Hyphae  $2-4\mu$  thick, producing oblong, bicellular, hyaline conidia ( $14-25 \times 5-6\mu$ ). The conidial stage degenerates as the perithecia grow mature. — Perithecia  $350-500\mu$  high,  $200-300\mu$  thick, obpyriform, laterally collapsing when dry, free or almost so, olive-greyish. — Peridium  $30-40\mu$  thick, very soft and tough; the major outer part textura globulosa, cells  $3-4\mu$  diam., thick-walled, coloured; the inner wall textura porrecta, hyaline, cells  $2-3\mu$  thick, graduating into the periphyses. — Asci in a dense basal cluster, aparaphysate; the periphyses are strongly developed, covering the inside of about the upper half of the perithecium; asci  $120-140 \times 5-6\mu$ , tapering below, ca.  $2.5\mu$  thick at the top, with a hemispheric, distinctly perforated cap-like structure (J—). — Spores as long as the asci, ca.  $1\mu$  thick, not constricted at the septa.

It is evident that this fungus is a member of *Clavicipitaceae*. It is very interesting in having free perithecia; all other *Clavicipitaceae* are stromatic.

The centrum structure fits very well to LUTTRELL's description of the centrum in the *Clavicipitaceae* (l. c., p. 61 and p. 96). It is open to discussion, however, whether this type of centrum is a representative of the *Xylaria*-type as supposed by LUTTRELL; it seems to me that a great hiatus exists between the *Xylaria*-centrum and the centrum of *Clavicipitaceae*, and that the free-ending hyphae in the perithecium of the latter type are periphyses.

The genus *Barya* is neither mentioned by NANNFELDT (1932) nor by GÄUMANN (1949) in their discussions of *Clavicipitaceae*.

*Ophionectria cerea* (BERK. & CURT.) SEAVER

On old *Diatrype disciformis* (HOFFM. ex FR.) FR., *Diatrype stigma* (HOFFM. ex FR.) FR., and *Bertia moriformis* (TODE ex FR.) DE NOT. (in the latter specimen soc. *Barya parasitica* FCK., see above); all on *Fagus silvatica*. Silkeborg Vesterskov 29. viii. 1953.

A description will be given here of this very remarkable fungus because it does not seem to have been adequately described previously:

Pseudothecia 180–250  $\mu$  diam., subisodiametric or slightly vertically elongated, never collapsing, the lower  $\frac{2}{3}$  forming part of a sphere, the upper  $\frac{1}{3}$  with an incrassated, ring-like cushion, in the centre of which is seen the small (25–30  $\mu$  thick and high), subcylindric papilla; colour a dull ochraceous yellow to brown (with age), a little darker in the depression round the papilla. – Peridium soft and brittle, very easy to cut, 25–30  $\mu$  thick in the bottom and sides, 50–55  $\mu$  thick in the subapical cushion, textura globosa-prismatica, cells 8–13  $\mu$  diam. (more flattened towards the centrum), thin-walled all through, angular in the main portion of the pseudothecium, globose (apparently with airy intercellular spaces) in the subapical cushion; papilla exclusively composed of vertical, parallel, subhyaline hyphae ca. 2  $\mu$  thick; centrum whitish, solid even in dry specimens. – Asci parallel, 70–80  $\times$  8–10  $\mu$ , subcylindric or somewhat ventricose, parabolically rounded at the 4–5  $\mu$  thick apex, bitunicate, apparently very thick-walled in the distal portion of the ascus. Spore-discharge has been observed in fresh material: The spores are liberated one by one after an apical rupture of the outer wall and a considerable elongation of the inner wall. Interascicular tissue dense, paraphysoid, filaments parallel or somewhat interwoven, hardly 1  $\mu$  thick. – Spores 3–4-seriate, 36–48  $\times$  2.5–3.5  $\mu$ , slenderly subfusiform,

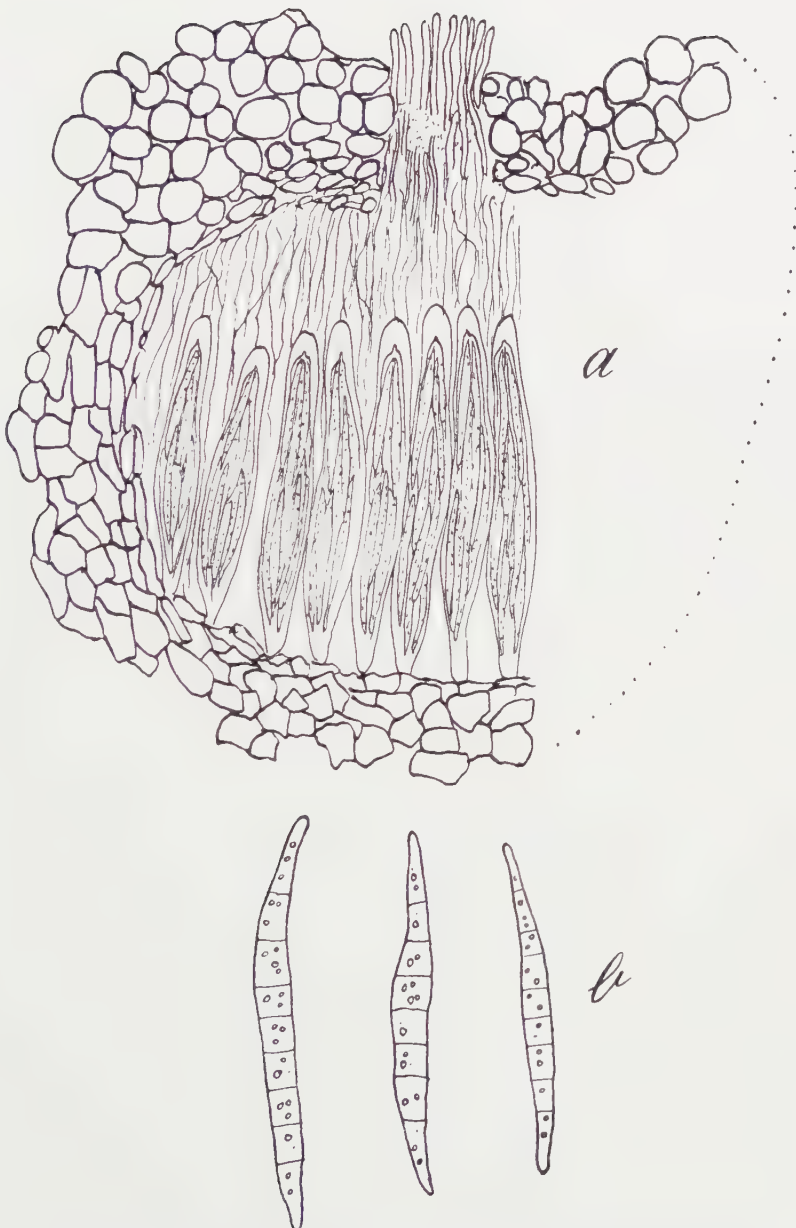


Fig. 2. *Ophionectria cerea* (BERK. & CURT.) SEEVER. — a) Section through a pseudothecium,  $\times 600$ . — b) Spores,  $\times 1150$ .

straight, curved or wavy, rounded at the  $0.5\text{--}1\ \mu$  thick ends, with small, scattered oil-drops, articulate by extremely delicate septa into  $3\text{--}4\ \mu$  long cells; hyaline or very slightly yellowish.

It appears from the description that this fungus is fundamentally different from other *Hypocreales*. This difference is obvious in all parts of the fungus: 1) The thick-walled, bitunicate ascus is very different from the thin-walled ascus of *Nectria*. 2) The asci are parallel and are kept together in parallel position when they are squeezed out of a fruit-body; in *Nectria* the asci are converging and assume a diverging position in squash mounts. 3) The permanently solid, not collapsing tissue of the centrum is—even when examined by low power magnification—very different from the strongly shrinking centrum tissue of *Nectria*. 4) The papilla, composed of parallel filaments continuous with the interascicular filaments, is very different from the palissade of diverging external periphyses in the *Nectria*-ostiole. 5) The peridium is particularly soft and brittle (the specific epithet "*cerea*" is very adequate) in contrast to the more or less tough and horny structure of the *Nectria*-perithecium.

It is beyond doubt that the present fungus belongs in *Ascoloculares*, whereas all other *Hypocreales* examined by me are *Ascohymeniales*. It can be placed in *Pseudosphaeriales*, but it is certainly doubtful whether the limits of *Pleosporaceae* can be extended as to comprehend this fungus which stands perfectly isolated among the *Pseudosphaeriales* I know.

The apical structure of the ascus is referred to the type "*à nasse apicale*" by CHADEFAUD (1942), i. e. the type characteristic of *Ascoloculares*. The case has been mentioned as an exception to the general rule that "*nasse apicale*" follows the bitunicate ascus of *Ascoloculares*. The present account goes to prove that no such exception exists here. In general, the typical bitunicate ascus seems to be found in all *Ascoloculares*, and in *Ascoloculares* only (cp. MUNK, 1954a).

This fungus has been reported from Denmark once (O. ROSTRUP, 1916, p. 8 sub. nom. *Calonectria belonospora* SCHROETER, evidently a synonym of *Ophionectria cerea*).

#### *Nectria modesta* v. H.

In September 1953 I examined an old, blackened banana which I found lying on the ground in a wood at Silkeborg. I found two perithecia of a *Nectria* with brownish, roughly punctate spores. I abandoned the material supposing the fungus to be a tropical species and because of the small amount of perithecia. A few days later I found the same *Nectria* in



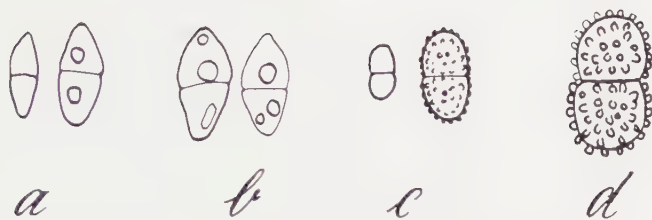


Fig. 3. Spores of a) *Nectria sanguinea* FR., – b) *Nectria magnusiana* REHM., – c) *Nectria modesta* v. H., and d) *Nectria cosmariospora* CES. & DE NOT. –  $\times 1150$ .

abundance on a half-decayed stump of *Fagus sylvatica*; it was then determined to *Nectria modesta* v. H. Since my first collections of this species I have found it several times on different substrata, always on wood previously attacked by other fungi or on the other fungi themselves. I have also found two specimens in the herbarium of Botanical Museum, Copenhagen (see below) to belong to *N. modesta*. A full list of the Danish specimens is given below. The fungus is certainly very common; it has been overlooked or misinterpreted in Denmark so far.

Fully ripe and well developed specimens of *Nectria modesta* v. H. are quite easily recognizable by their brownish, rough spores (which measure  $10-11 \times 5-6 \mu$ ). The fungus is often found in a less developed state with smaller ( $8-9 \times 3.5-4 \mu$ ), almost hyaline and smooth spores. In such cases the shape of the spores is a sufficient distinctive character against *N. sanguinea* FR. (= *N. episphaeria* (TODE ex FR.) FR.):

*Nectria sanguinea* FR.: Spores not constricted at the septum, rather narrowly rounded at the ends.

*Nectria modesta* v. H.: Spores somewhat constricted at the septum, broadly rounded at the ends.

*Nectria modesta* is a member of a group of the genus which is well characterized by the hypersaprophytic ecology, by a peculiar pattern of variation in the spores (see Fig. 3), and by the well-developed ostiole combined with a thin peridium in the body of the perithecium. The other Danish members of this group are *Nectria sanguinea* FR., *Nectria magnusiana* REHM, and *Nectria cosmariospora* CES. & DE NOT. (cp. further MUNK, 1954b).

Danish specimens of *Nectria modesta* v. H.:

1) On rotten wood. Fyn: Klingstrup (E. ROSTRUP sub nom. *Nectria sanguinea* (SIBTH.) FR.). – 2) On bark of *Quercus*, erumpent in dense clusters in fissures in the bark, soc. *Diaporthe leiphaemia* (FR.) SACC.

Sjælland: Rudehegn (J. LIND sub nom. *Nectria episphaeria* (TODE) FR. on *Diaporthe leiphaemia*). – 3) On the saw-cut surface of a stump of *Fagus silvatica*. Jylland: Silkeborg Vesterskov (A. M.). – 4) On (and among) living *Lasiosphaeria spermoides* (HOFFM.) CES. & DE NOT. on a decaying stump of *Fraxinus excelsior*. Jylland: Lysbro Skov near Silkeborg (A. M.). – 5) On *Lasiosphaeria spermoides* on a stump of *Fagus silvatica*. Jylland: Silkeborg Vesterskov (A. M.). – 6) On a rotten, hardly determinable stump, soc. *Debaryella gracilis* MUNK n. sp. (see below). Jylland: “Lunden” at Silkeborg (A. M.).

*Debaryella gracilis* n. sp.

*Peritheciis* 170–200  $\mu$  diam., *subliferis*, *hyalinis fere vitreis*, *verticaliter elongatis*, *ostiolis* c. 50–60  $\mu$  *crassis*, *papillatis vel subcylindraceis praeditis*. – *Peridio molle*, *ceraceo*, *hyalino*, *pellucido*, *structura indistincta*. – *Ascis* 80–95  $\mu$  p. sp.  $\times$  c. 8  $\mu$ , *cylindraceis*, *breve stipitatis*; *structura apicale asci ut in multitudine Diaporthacearum*; *ascosporis dejectione dimidii distalis asci liberatis*. – *Ascosporis biseriatis*, *rotundato-fusiformibus*, *saepe leniter curvatis*, 27–34  $\times$  3–4  $\mu$ , *saepius (pseudo-)septis 6-cellularibus*.

*In trunculo putrido specie incerta, socie Nectria modesta* v. H. – Dania: “Lunden” *prope urbem Silkeborg*, 2. iv. 1954. (Legit auctor).

*Perithecia* 170–200  $\mu$  diam., slightly vertically elongated, tapering above; ostiole 50–60  $\mu$  thick, papillate (or more elongated: subcylindric); the perithecia are free or almost so, sparsely gregarious in and among small crowds of *Nectria modesta* v. H.; in the fresh material they were whitish-hyaline; in the dried material they are of an undeterminable dirty wood-colour, somewhat collapsed and very difficult to see, even under a good stereomicroscope. – *Peridium* extremely soft, waxy, probably about 20–30  $\mu$  thick, hyaline, in the outer part of a quite indistinct, apparently originally small-celled texture; in the inner portion of the peridium may be distinguished a small-celled tissue with 2–3  $\mu$  large, thin-walled cells; the ostiole is built up of slightly diverging cell-rows (the same tissue as in the inner perithecial wall); porus narrow, filled with strongly ascendent, thin periphyses. – *Asci* subparallel, 80–95  $\mu$  p. sp.  $\times$  ca. 8  $\mu$ , cylindric, short-stipitate; apical structure of the *Diaporthe*-type, visible in optic section as two small, refractive spheres near the centre of the hemispherically rounded apex of the ascus. (Spore-discharge was observed in fresh material: The distal half of the ascus breaks off along a neatly circular, apparently preformed zone. This method of spore liberation is the same as is described by INGOLD (1951) for the two aquatic *Pyreno-*

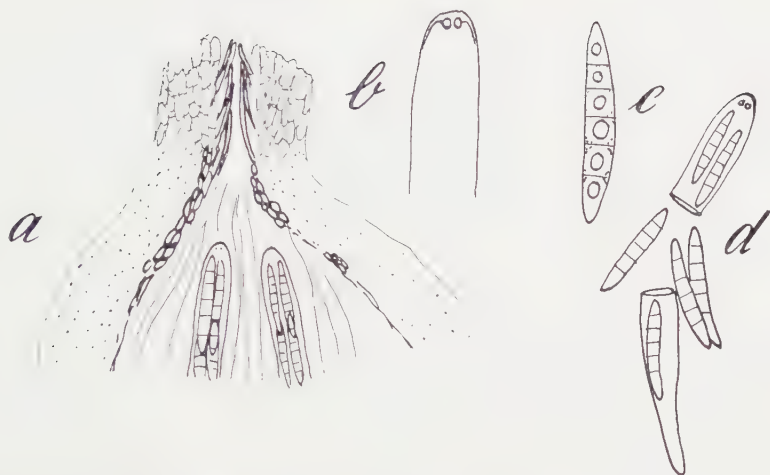


Fig. 4. *Debaryella gracilis* n. sp. — a) Median section through the upper part of a perithecium,  $\times 300$ . — b) Ascus-top,  $\times 880$ . — c) Spore,  $\times 880$ . — d) Ascus-top in moment of spore-discharge,  $\times 500$ .

*mycetes*, *Ceriospora caudae-suis* INGOLD and *Ophiobolus typhae* FELTG.). — Paraphyses rather abundant, filiform, very thin-walled. — Spores biserial,  $27-34 \times 3-4 \mu$ , rounded-fusiform, slightly curved, (5-)6(-7)-celled, slightly or not constricted at the very inconspicuous septa (which probably ought to be termed pseudo-septa), hyaline, with a large oil-drop in each cell.

The genus *Debaryella* v. H. is thoroughly discussed by WEESE (1919, p. 17-23). Two species are previously known, viz. *D. hyalina* v. H. (type species of the genus) and *D. vexans* v. H., both "parasitic" and immersed in old stromata of *Eutypa* spp., and both with uniseriate, four-celled spores. The present fungus differs from WEESE's diagnosis of the genus in the three emphasized characters.<sup>1)</sup> It is hardly possible, however, to place the fungus anywhere else; and the peculiar structure of the peridium—which fits very well to WEESE's descriptions—seems to me to be a strong indication of a relationship. Further, the ecological difference between the present fungus and the two species of *Debaryella* is not significant at all, as pointed out in previous papers (MUNK, 1950, 1953): A fungus which is found on or in old and empty fruit-bodies of other fungi should not be termed "parasitic". This particular ecology is rather

<sup>1)</sup> Another specimen of the same species shows totally immersed perithecia (Silkeborg Sønderkov 30. March 1954, on rotten wood of *Acer pseudoplatanus*, soc. *Platystomum compressum* (PERS.) TREV.).

a "hyper-saprophytism"; and it is often seen that saprophytic fungi of second or higher incidence are closely related to fungi which, more or less obligately, occur on dead fungi (e. g. *Herpotrichiellaceae*, cp. MUNK, 1953, p. 131; a group of the genus *Nectria*, cp. MUNK, 1954b, see the present note on *Nectria modesta* v. H.).

A revision of the generic diagnosis of *Debaryella* v. H. appears to be necessary:

*Debaryella* v. H., emend. MUNK

*Diaporthaceae*. Peritheciis clavis, subhyalinis,  $\pm$  immersis, typice ostiolis  $\pm$  elongatis praeditis. Peridio mollissimo, textura partim indistincta, partim parvicellulari. Ascosporis uni- vel biseriatis, muticis, hyalinis, 4-cellularibus vel 6-7-cellularibus. – Hypersaprophyta: In stromatibus vetustis *Pyrenomycetum* aliorum vel ad lignum myceliis fungorum aliorum partim destructo.

WEESE (l. c., p. 22) suggests that the group of immersed, "parasitic" *Hypocreales* is polyphyletic, and that no close relationship exists between the genera mentioned by him. These fungi are very inconspicuous and rarely found. I have only seen the present species, and little can be concluded at present. But it should be pointed out that one of the genera mentioned by WEESE: *Cryptonectriopsis* (v. H.) WEESE (spores one-celled) is placed in *Gnomoniaceae* by v. ARX (1951, p. 267 and Fig. 3), i. e. among *Diaporthales*; and that v. ARX's figure shows a fungus with a very small-celled peridium and a "bipunctate" ascus-top, just like the present fungus. The group may appear, after all, to constitute a morphologically and ecologically well characterized group of the *Diaporthaceae* sensu meo (= *Diaporthales* sensu auctt. plur.).

No wonder that this fungus has remained undiscovered so far. It was reasonably conspicuous in the fresh material; but I spent about half an hour in search of the fungus on the dried piece of wood with which I had become well acquainted during my first examination of the material, although I used a stereomicroscope with 30 times magnification!

### Literature.

- VON ARX, J.-A., 1951: Ueber die Gattung *Laestadia* und die *Gnomoniaceen*. – *Antonie van Leeuwenhoek* 17: 259–272.  
 CHADEFAUD, M., 1942: Études d'asques II. – *Revue de Mycologie* 7: 57–88.  
 GÄUMANN, E., 1949: Die Pilze. (Basel). – 382 pp.  
 INGOLD, C. T., 1951: Aquatic Ascomycetes: *Ceriospora caudae-suis* n. sp. and *Ophiobolus typhae* FELTGEN. – *Trans. Brit. Myc. Soc.* 34, 2: 210–215.

- LUTTRELL, E. S., 1951: Taxonomy of the Pyrenomycetes. – Univ. Miss. Stud. *XXIV*, 3, – 120 pp.
- MÜLLER, E. & VON ARX, J.-A., 1950: Einige Aspekte zur Systematik pseudo-sphaerialer Ascomyceten. – Ber. d. Schw. Bot. Ges. *60*: 329–397.
- MUNK, A., 1950: Some remarks on relations between stromatic and nonstromatic Pyrenomycetes. – VII. Bot. Congress, Stockholm.
- 1953: The System of the Pyrenomycetes. – Da. Bot. Arkiv *15*, 2. 163 pp.
- 1954a: The bases of the systematic relationships of the Pyrenomycetes. – VIII. Bot. Congress, Paris.
- 1954b: An anatomic study in the genus *Nectria* Fr. with remarks on the pattern of variation within the genus. – VIII. Bot. Congress, Paris.
- 1954c: A Flora of Danish Pyrenomycetes (in press).
- NANNFELDT, J. A., 1932: Studien über die Morphologie und Systematik der nicht-lichenisierten, inoperculaten Discomyceten. – Nov. Act. Reg. Soc. Sc. Upsaliens. *8*, 2. 368 pp.
- ROSTRUP, O., 1916: Bidrag til Danmarks Svampeflora I. – Da. Bot. Arkiv *2*, 5.
- WEESE, J., 1919: Beiträge zur Kenntnis der Hypocreaceen. – Sitzb. d. K.-K. Akad. d. Wiss. zu Wien. Mat.-Nat. Kl. I, *128*, 9–10, 61 pp.



## Vorsø set fra luften

Af D. MÜLLER

I 1929 blev Vorsø købt af HERLUF WINGE's legat. Derved opstod mulighed for at følge udviklingen fra græsmark og forstmæssig drevet skov til urskov. Vorsø skove vil langsomt erobre hele det fredede areal på øen, der igen vil blive dækket af urskov, som den var det før mennesker kom dertil.

Professor, dr. KNUD JESSEN har siden 1931 siddet i Vorsøs tilsynsråd og år for år fulgt ændringen i floraen på den dejlige lille ø i Horsens fjord. De luftfotografier, der er gengivet her, viser Vorsø som professor JESSEN kender øen.

Da Vorsø skove udvikler sig til urskov, er det af vigtighed at følge denne udvikling også med rent forstmæssige målinger. Vorsø skove er blevet takseret i maj 1952 (se MÜLLER & NIELSEN, 1953), og bør takseres hvert 10. år fremefter. De luftfotos, der gengives her, er taget i august 1953 og november 1953 og supplerer taksationen i 1952.

Fig. 1 viser Vorsø set fra sydvest. I forgrunden ligger den vestlige udmark, hvor endnu kun få træer har slået rod. Nederst til venstre i billedet er den lille trægruppe Vestre Remise med poppel og rødell i EII og EIII (Betegnelserne henviser til det kvadratnet, der er indlagt på kortet over Vorsø hos MÜLLER & NIELSEN). Skarvekolonien i Vesterskovens nordvestlige hjørne, CIV og DIV, kan ikke ses på luftfotografiet. Nederst til højre i forgrunden bemærkes den ganske lille trægruppe, der kaldes tepotten.

Fig. 2 viser Vorsø set fra sydøst. Forrest i billedet står gråpoplerne sydøst for Østerskov, EXI og FXI. Særlig tydelig er den interessante selvsåning af ær, en 23-årig stangskov i DXI, øst for Østerskov.

Mellem Østerskov og den lille trægruppe Østre Remise, CXI, der ses længst til højre på fig. 2, har der allerede indfundet sig langt flere småtræer end i den vestlige udmark. Det er de fremherskende vestenvindes skyld. Hejrekolonien i Østerskov er ikke synlig på luftfotografiet.

Fig. 3 er et vinterbillede af Vorsø set fra sydøst.



Fig. 1. Vorsø set fra sydvest, august 1953.



Fig. 2. Vorsø set fra sydøst, august 1953.



Fig. 3. Vorskø set fra sydøst, november 1953.

### Litteratur.

MÜLLER, D. & JÖRGEN NIELSEN, 1953: Vorskø Skov. *Botanisk Tidsskrift* 50, 35–55.

## The Genus *Leucopaxillus* in Denmark

By F. H. MÖLLER

Ever since ELIAS FRIES created his ingenious system on the *Agaricaceae* and other higher fungi, taxonomists have attempted to improve it. It was found that in applying exclusively macroscopic characters, for instance the nature of the flesh and the veil, the colour of the spore powder, the insertion of the gills etc., FRIES had disregarded the natural relationship of the species. By microscope and chemical reactions, etc. new and often more convenient and natural genera were created, sometimes merely by rearranging the sections. Several of FRIES' genera comprised well-defined sections which easily could be separated as good, independent genera (for instance *Cystoderma*, *Melanoleuca* and *Conocybe*).

It is more difficult to accept the genera which are formed by combination of two or three groups of species from different genera (for instance *Agrocybe*, formed by related *Naucoria*- and *Pholiota*-species), although improvements may be achieved also in that way.

The least acceptable situation arises if taxonomists, when creating new genera, pay more regard to microscopic details, than to good, outer characters. A suitable combination of old-fashioned and modern methods in the building of the future agaric system is therefore advisable, in order to prevent mycologists from losing contact with the general public which means so much to mycology.

The genus *Leucopaxillus* treated here is an example of a genus which is still in the melting-pot, being built up mainly on modern principles. It was created in 1925 by BOURSIER on the basis of two white-spored species which were originally referred to *Tricholoma* and *Clitocybe*, namely: *Tricholoma pseudoacereum* COST. & DUF. and *Clitocybe paradoxa* COST. & DUF. In addition to several macroscopic points of similarity these two fungi also have the common character that the spores are stained blue by

iodine and then present delicate, but distinct, warts under an immersion lens.

Later, more than ten other species have been added to this genus, but the taxonomists still disagree about the correct delimitation of the genus. SINGER & SMITH (1943), in their excellent monograph on *Leucopaxillus*, included the so-called *Aspropaxillus*-group, which includes *Clitocybe gigantea*, and has smooth, slightly amyloid spores. KONRAD & MAUBLANC, however, consider this species as a genuine *Clitocybe*, but like MOSER—they include in *Leucopaxillus* another smooth-spored species: *Tricholoma spinulosum* KÜHN. & ROMAGN. (— *Tricholoma guttatum* sensu LANGE).

In the following small survey, which comprises only Danish species, the last-mentioned species, as well as *Clitocybe gigantea*, have been included.

### *Leucopaxillus*.

Robust or medium-size, white-spored species, with at first involute, often grooved or ribbed, pubescent margin, gills decurrent or rounded, flesh compact, hyphae with numerous clamp connections, spores more or less amyloid, often rough.

### Key to Danish species.

- A. Spores smooth, slightly amyloid. Flesh mild with sweetish smell.
  - B. Gigantic, whitish species, resembling *Clitocybe geotropa*, but with short stem and sulcate margin of cap, and other spores. . . . . 1. *L. giganteus*
  - B. Medium-size species with *Tricholoma* characters. Cap clay-coloured, with numerous small, brown, appressed scales and hairy margin. Stem with rooting base. Under *Ulmus* . . . . . 2. *L. spinulosus*
- A. Spores rough, distinctly amyloid. Three of the species have more or less bitter flesh.
  - B. Gills strongly decurrent, at first light reddish. Resembles *Clitopilus prunulus* or *Clitocybe pithyophila*. No cheilocystidia . . . . . 3. *L. rhodoleucus*
  - B. Gills rounded or slightly emarginate, often with decurrent tooth. The edge of the gill lined with hyphae.
    - C. Gills lemon-yellow. Very large species from deciduous woods, with markedly thick and ovate stem and thick, compact flesh . 4. *L. tricolor*
    - C. Gills white. Stem almost cylindric. Species from coniferous woods.
      - D. Cap red-brown. Flesh very bitter. . . . . 5. *L. amarus*
      - D. Cap white, strongly whitish tomentose. Flesh less bitter or almost mild. . . . . 6. *L. alboalutaceus*



1. *Leucopaxillus giganteus* (FR.) SINGER

Syn.: *Clitocybe gigantea* FR. – *Paxillus giganteus* FR. – *Aspropaxillus giganteus* (FR.) KÜHN. & MAIRE.

Icon.: FRIES, Ätl. och Gift. Sv., t. 86. – LANGE, Fl. Ag. Dan., t. 33 F.

Expanded cap 10–25 cm. broad, whitish, soon becoming alutaceous, when dry floccose, sometimes slightly cracked-squamose, early deeply cup-shaped, without umbo. Margin pubescent, thin, strongly involute, radiately furrowed by shallow canals. Gills already early pale yellow, narrow, very crowded, deeply decurrent, often forked at the stem. Stem 4–8 cm.  $\times$  3–4 cm., white, later yellowish, almost cylindric, floccous or pubescent, solid. Flesh whitish or yellowish, tough, mild. Smell sweetish aromatic as in *Clitocybe geotropa* (according to other statements: farinaceous). Spore powder white.

Spores ellipsoidic, smooth (NÜESCH: glatt bis rauhlich), with 1–2 oil-drops, slightly amyloid, 5.5–7  $\times$  3.5–4  $\mu$ . Basidia 4-spored, 26–32  $\times$  6  $\mu$ . No cheilocystidia.

In light deciduous and coniferous woods, also in lawns in parks, often in large fairy-rings and killing the grass. Till now not found in Lolland-Falster. Here and there in Fyn and Sjælland, perhaps particularly frequent in the latter island.

Sjælland: Frederiksborg Slotspark 1933; Enemærket at Næsbyholm 16. Sept. 1934, (material described above); Knudsskov at Vordingborg 30. Aug. 1953, here found on pure needle-bed (*Picea*); consequently it is not parasitic on grass; Viemose Skov 10. Sept. 1953. Other finds: Sjælland: Slagelse Skov 1890, SEVERIN PETERSEN; Charlottenlund Skov 3. Sept. 1931 and later, E. DEHN, in Friesia; Grib Skov 28. Sept. 1947 (Friesia); In a meadow at Gentofte, K. BÜLOW; J. P. JENSEN in litt.: "In the course of time I have met with it in Gelskov and in Furesøparken at Holte, in Ganløse Ore (29. Aug. 1948, Friesia), at Hornbæk and at Kvistgård, also in Jægersborg Dyrehave (6 localities) where it was found from 7. Aug. to 26. Sept.; 2 fairy-rings were seen in 1940, of which the one found on 14. Aug. 1940 contained 200 individuals in 18 m. broad ring, a very imposing view!" – Fyn: Dalum, Sept. 1905–07, JAK. E. LANGE. – Jylland: (AKSEL B. KLINGE in litt.): Fussingø 8. Sept. 1941 (fairy-ring); Gl. Estrup 1. Sept. 1951 (under *Corylus*, gregarious); Fjeld Skov at Auning 30. Sept. 1951 (fairy-ring). – Sverige: Karlstad 8. Sept. 1937, H. SVENSON; Rättvik 5. Sept. 1940 (B. CORTIN in Friesia).

It is still an unsolved problem whether *L. giganteus* and *C. candidus* (BRES.) are specifically distinct or not. The last species is described as having milk-white cap with smooth margin, white gills, and narrower spores than in *L. giganteus* (see picture and description in NÜESCH: Die Trichterlinge, and in BRESADOLA: Icon. Myc. t. 172). While some mycologists (SINGER & SMITH, NÜESCH a. o.) consider *L. candidus* to be an

autonomous species or at any rate a mountain-variety of *L. giganteus*, most workers sharply oppose this view (ROMELL, SETH LUNDELL, KONRAD & MAUBLANC, JAK. E. LANGE a. o.). SEVERIN PETERSEN (according to his diary: Find in Bromme Plantage 3. Sept. 1890) and POUL LARSEN (Diary: Langesø Skov, Fyn, 14. Sept. 1930), and KOLDERUP ROSENVINGE (Bot. Tids. 37: 159-160. 1920, Jægersborg Dyrehave, believe to have found *L. candidus* in this country. The author is afraid that the mentioned characters of this species are inconstant. The spores of *L. giganteus*, for instant, vary strongly in form and may be as narrow (see spore measurements above) as in *L. candidus* (BRESADOLA: 7-8  $\times$  3-4  $\mu$ ) and (according to SINGER & SMITH) the margin of the cap may, in exceptional cases, be smooth in *L. giganteus* and furrowed in *L. candidus*; these authors therefore point out the white gills as being a particularly distinctive character for *L. candidus*. Further examinations are therefore very necessary.

## 2. *Leucopaxillus spinulosus* KÜHN. & ROMAGN. Fig. 1a.

Syn.: *Tricholoma guttatum* BARLA (nec al.) in LANGE: Fl. Ag. Dan. — *Tricholoma spinulosum* KÜHN. & ROMAGN.

Icon.: LANGE: Fl. Ag. Dan., pl. 24 E.

Cap 5-6 cm. broad, light clay-brown, smooth at the centre, but further out covered with small, appressed dark-brown scales, convex, the middle being flattened or slightly umbonate; margin thin, at first shortly involute and hairy squamulose; pellicle thick and separable. Gills white or whitish yellow, ochraceous when touched, rather broad, crowded, rounded behind, almost free. Stem 4-5 (-12) cm.  $\times$  10-15 mm., white, but becoming strongly yellow-brown, specially downwards, apex slightly thickened, base more or less rooting, glabrous, round or somewhat compressed, solid. Flesh whitish, ending in yellow in the stem, compact, especially in the stem; taste mild, not bitter, not farinaceous, smell indeterminably sweetish, when cut, however, distinctly spermatic (LANGE: "sweetish-aromatic, slightly farinaceous, but faint", KÜHNER & ROMAGNESI: "Odeur légère, rappelant celle d'*Inocybe Bongardii* ou de girofles"). Spore powder white.

Spores ovate or rounded ovate, with an oblique apiculus and large gutta, amyloid (KÜHNER & ROMAGNESI), smooth, 4.5-5(-7)  $\times$  3-3.75  $\mu$  (individuals from LANGE) or 5-6  $\times$  3.5-4  $\mu$  (19. Oct. 1938). Basidia 4-spored, 25-36  $\times$  5-7.5  $\mu$ . No cheilocystidia.

Danish finds: JAK. E. LANGE 4. Oct. 1932, Carolinekilde at Odense in park with two fruit bodies on bare soil under *Ulmus*. It was sent to the author who on 19. Oct.

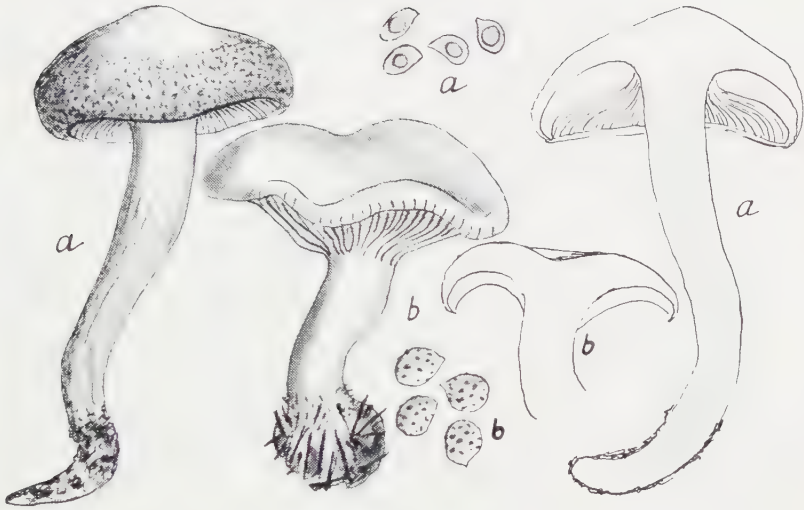


Fig. 1. a) *Leucopaxillus spinulosus*. Fruit-body with section (1:2), spores (1000:1). b) *L. rhodoleucus*. Fruit-body with section (1:2), spores (1000:1). a) from Vordingborg, b) from Kastrup Storskov.

1938 found it again in one long-stemmed specimen with 2–3 cm. long “tap-root” on a grass verge under *Ulmus* in Vordingborg. – AXEL B. KLINGE 27. Sept. 1953: Ajstrup Skov at Hadsund (Jylland) under young, self-sowed *Acer pseudoplatanus* and *Ulmus glabra* (in litt.).

Seems very rare and is attached to *Ulmus*.

This rather unknown species, found i. a. in France, and Switzerland and elsewhere, is not easy to classify. KÜHNER & ROMAGNESI originally referred it to *Leucopaxillus*, but in their last work (1953) to *Tricholoma*. In future finds it should be ascertained whether it is directly attached to *Ulmus* roots.

### 3. *Leucopaxillus rhodoleucus* (ROMELL) KÜHN. Fig. 1b.

Syn.: *Agaricus* (*Clitocybe*) *rhodoleucus* ROMELL. – *Lepista rhodoleuca* (ROMELL) R. MAIRE.

Icon.: R. MAIRE in Bull. Soc. Myc. Fr. 40, pl. XX, Figs. 2–7. The spores are shown more longish than in Danish and Swedish finds.

Cap 6–8 cm. broad, when dry beautifully white, slightly flesh-coloured when moist, glabrous, flatly convex, somewhat depressed in the middle, margin radiately sulcate, at first involute. Gills more or less flesh-coloured as in *Clitopilus prunulus*, rather narrow and crowded, deeply decurrent.

Stem 5 cm.  $\times$  15 mm., almost cylindric, concolorous with the cap, glabrous, base somewhat incrassated and condensing the needles, curved, elastic, solid. Flesh white; slightly acidulous but not farinaceous smell; taste mild. Spore powder white.

Spores globosely ovate, amyloid, rough,  $7-8 \times 5-6 \mu$ , mostly  $7 \times 5 \mu$ . Basidia 4-spored,  $34-38 \times 7-8 \mu$ . No cheilocystidia.

New to Denmark, and only found in Sjælland, in Kastrup Storskov 4. Nov. 1918, 4 fruit-bodies under *Picea* and *Betula* (Sp.  $8.25 \times 5.5 \mu$ ) and 15. Nov. 1953 in Lolland in Fuglsang Storskov, 1 fruit-body under *Picea* (L. DOSSING leg.). 1 fruit-body was gathered by mycophagists at Naskov and handed for determination to G. EBBESEN 6. Oct. 1935.

The species resembles *Clitocybe pithyophila*, to which also SEVERIN PETERSEN referred the find from Kastrup Storskov, but it is not identical with *Rhodopaxillus panaeolum* as BRESADOLA maintained.

#### 4. *Leucopaxillus tricolor* (PECK) KÜHN. Fig. 2a.

Syn.: *Tricholoma tricolor* PECK. – *Tricholoma pseudoacerbum* COST. & DUF. – *Leucopaxillus pseudoacerbus* (COST. & DUF.) BOURS. – *Lepista pseudoacerba* (COST. & DUF.) KONR. & MAUBL.

Cap 10–15 cm. broad, light ochraceous reddish or dirty ochraceous, towards the margin lighter, dull, slightly tomentose, compact, flatly convex, often at last quite repand, without umbo; margin strongly involute, distinctly tomentose, sulcate, at last very repand. Gills lemon yellow, narrow, especially near margin, crowded, rounded or at last slightly decurrent, anastomosing, edge denticulate, flocculose. Stem short and thick as in *Boletus edulis*, up to 10 cm.  $\times$  10 cm., white, everywhere whitish flocculose, with rigid and firm pellicle, solid or somewhat hollow. Flesh white, compact, smell somewhat disagreeable almost as in *Tricholoma lascivum*, taste farinaceous, bitterish. Often bitten by slugs. Spore powder white.

Spores ovate, with large drop, amyloid, rough,  $6-7 \times 4-5 \mu$  (1943) or  $6 \times 4 \mu$  (1950). Basidia 4-spored,  $34-36 \times 7.5-8 \mu$ . At the margin numerous narrow, hyaline and sinuous hyphae which are  $2-3 \mu$  broad at apex and  $4.5 \mu$  broad at base. Young individuals from the find of 1950 had capitate hyphae at the edge of the gill, apex  $4-7 \mu$  broad, some fertile basidia were seen among the hyphae.

Also new to Denmark. Rare. Only found twice in Denmark, both times in Møens Klinteskov (a wood growing on white lime), 28. Aug. 1943 (C. H. WESTERGAARD, 1 old specimen) and 20. Aug. 1950 (2 young fruit-



Fig. 2. a) *Leucopaxillus tricolor*. Fruit-body with section (1:2), spores (1000:1), and hyphae from the gill edge (500:1). b) *L. alboalutaceus*. Fruit-body with section (1:2), spores (1000:1), and hyphae at the edge of the gill (500:1). a) from Møens Klint 1950, b) from Hannenau Skov <sup>3</sup>/<sub>11</sub> 1935.

bodies under *Fagus* and *Quercus* at Hotel Storeklint, west of Sommer-spiret).

As the vigorous growth and the furrowed margin of the cap suggest *Tricholoma acerbum*, CONSTANTIN & DUFOUR named it *T. pseudoacerbum*. It should be searched in localities rich in lime in Jylland.

MOSER did not include it in his "Kleine Kryptogamenflora von Mitteleuropa", but it is known in U.S.A., where PECK described it already in 1888, some years before it was found in France.

### 5. *Leucopaxillus amarus* (FR.) KÜHN.

Syn.: *Clitocybe amara* (ALB. & SCHW.) FR. – *Tricholoma amarus* (FR.) REA. – *Lepista amara* (FR.) R. MAIRE. – *Leucopaxillus amarus* f. *typicus* sf. *minor* SING. & SMITH. – *Tricholoma guttatum* FR. non SCHAEFF.

Icon.: KÜHNER in Bull. Soc. Myc. Fr. 44, pl. 24, 1928. – LANGE, Fl. Ag. Dan., pl. 24 D.

Cap 5–8 cm. broad, red-brown, towards the margin lighter, densely tomentose, flatly convex, later subplano-depressed, sometimes subumbonate; margin involute, distinctly tomentose, distantly furrowed, later spreading and lobate. Gills white, when touched and in age spotted fulvous, attenuated in front, much broader behind, very crowded, rounded adnate, often with decurrent tooth, thin, sometimes forked, edge floccose. Stem 3–5 cm. × 10–15 mm., base thicker, white, gradually with a slight flesh-coloured tinge, dull, pruinose-pubescent, pithy, be-



coming hollow in lower part, base connecting the needles. Flesh white, or slightly yellowish in the stem, compact, tough in the bark of the stem, taste farinaceous and bitter like quinine, smell somewhat unpleasant almost as *Tricholoma lascivum*, when cut farinaceous-acidulous. Spore powder white.

Spores roundish, with drop, amyloid, rough,  $3.75-5 \times 3.5-4.25 \mu$  (10. Sept. 1922) or  $4-4.5(-5) \times 3.5-4 \mu$  (29. Oct. 1935). Basidia 4-spored,  $26-28 \times 6-7 \mu$ . The edge of the gill fringed with numerous flexuous, hyaline, nettlehair-shaped or cylindric hyphae, some branched, at base  $4-6 \mu$  thick. The projecting part  $30-40 \times 2 \mu$ .

Rare. In old *Picea*-wood, growing in fairy-rings. Hydesby Skov in Lolland 10. Sept. 1922 (2 mycelia), and 29. Oct. 1935 in the same locality from which JAK. E. LANGE received fruit-bodies for illustration in Fl. Ag. Dan. — The latest finds, by AXEL B. KLINGE (in litt.): Jylland: Dronninglund Storskov under *Picea* 10. Sept. 1950 and Blichers Plantage at Spentrup under *Picea* 2. Nov. 1952.

6. *Leucopaxillus alboalutaceus* (MOLL.) MOLL. comb. nov. Fig. 2b.

Syn.: *Tricholoma amarum* var. *alboalutaceum* MÖLL. in LANGE in Fl. Ag. Dan. — *Lepista alboalutacea* (MÖLL.) MÖLL. & SCHÄFF. in Ann Myc. 38: 118-120. 1940, with short diagnose.

Cap 3-7 cm. broad, white, at last with alutaceous tinge in the middle, when touched ochraceous spotted, dull, very distinctly white-flocculose, becoming naked, convex and then flatly depressed, without umbo; margin pubescent, at first involute, later spreading, often at first shortly ribbed. Gills white, later yellowish, narrow, very broad behind, rounded adnate with small decurrent tooth, very crowded and thin, often cracking in the flocculose edge. Stem 3-5 cm.  $\searrow$  10 mm., white, later becoming yellowish, dull, powdery-flocculose, base thick and encircled by needles, often deeply fastened, pithy, below hollow. Flesh white or slightly yellowish, especially in the bark of the stem, compact, tough in the stem, varying from very bitter, to almost mild (SCHÄFFER). Smell as in *L. amarum*, unpleasant aromatic, when broken farinaceous acidulous, often almost as in *Tricholoma lascivum*. Spore powder white.

Spores rounded, with drop, amyloid, rough,  $4.5-6.25 \times 3.75-4.5 \mu$  (10. Aug. 1930) or  $4-4.5 \times 3-3.5(-4) \mu$  (3. Nov. 1935). Basidia 4-spored,  $20-31 \times 5-7 \mu$ . The edge of the gill lined with hyphae similar to those of *L. amarum*, 1-3  $\mu$  thick, inflated below.

Here and there but perhaps often overlooked. In old *Picea*-woods near the base of trees where the ground is rather dry. It is never found together with the closely related *L. amarum*, which is rare in Denmark.

Some finds: Lolland: Maltrup Skov 10. Aug., 26. Oct. 1930 and 30. Aug., 20. Sept. 1931. — Falster: Vennerslund 2. Sept. 1923; Horreby Lyng 4. Sept. 1931; Lidstrup Lyng several times, latest 3. Nov. 1935; Hannenav Skov 22. Sept. 1931, 3. Nov. 1935, rather frequent; Lindsøen at Nykøbing 20. Oct. 1931. — Jylland: Lundbjerg Bakker 29. Sept. 1945. — Sjælland: Jægersborg Dyrehave 14. Oct. 1945 and 16. Oct. 1949 under an old *Larix* at Skovridergården (J. P. JENSEN in litt., Friesia).

SINGER & SMITH (l. c.) think that it is a form of *L. amarus* and write: "Since F. H. MÖLLER was the collector of LANGE's material of *L. amarus* f. *typicus* he must have known this species, and therefore we are inclined to believe that var. *alboalutaceus* is nothing more than a very pale form of *L. amarus*". That is an error; the very fact that MÖLLER found both of them enables him, better than anybody else, to see that *L. alboalutaceus* is more than a mere form of *L. amarus*. In this connection it may be appropriate to quote what J. SCHÄFFER wrote about *L. alboalutaceus* (l. c.): "Auf den Gedanken, dass sie unter *amara* als deren blasse, weisse Varietät zu suchen wäre, wäre ich schwerlich gekommen, wenn ich nicht von MÖLLER persönlich darauf hingewiesen worden wäre" etc.

It will be seen that the author has had the extraordinary luck to come across these rare species or to have have them sent to him by mere chance. This little article is a modest attempt to repay the kindness shown by nature and kindly friends. If it may also help to stimulate the interest in and the study of these rare and reticent species I shall have achieved my purpose.

### Literature.

In addition to the usual large hand-books the following papers have been consulted:

- BOURSIER, M., 1925: *Leucopaxillus* nov. gen. Bull. Soc. Myc. Fr. 41: 391–393.  
 BUCHET, S. & COLIN, H., 1913: *Le Tricholoma pseudo-acerbum* Cost. & Duf.—  
 espèce litigieuse—et son pigment. Ibid. 29: 162–164.  
 COSTATIN, J. & DUFOUR, L., 1895. Pe. suppl. nouv. flor. Champ., 259, 262. (*Trich.  
 pseudoacerbum* and *Clit. paradoxa*).  
 — 1927: Note sur le *Tricholoma pseudoacerbum* Cost. & Duf. Ibid. 43: 117–118.  
 DUMÉE, P., 1926: Notes de Mycologie pratique. Ibid. 42: 173–174.  
 — 1927: Note sur les *Tricholoma pseudo-acerbum*, *Guernisaci* et *militare*. Ibid.  
 43: 263–264.  
 MAIRE, R., 1926: Études mycologiques. Ibid. 40: 293–317.  
 SCHÄFFER, J., 1940: Die authentischen *Russula*-Arten von El. Fries, Anhang:  
*Lepista alboalutacea*. Ann. Myc. 38: 118–120.  
 SINGER, R. & SMITH, A. H., 1943: Monograph on the Genus *Leucopaxillus* Boursier.  
 Pap. Mich. Acad. Science, Arts and Letters 28: 85–132. 1942, publ.  
 — 1947: Additional Notes on the Genus *Leucopaxillus*. Mycologia 39: 725–736.

## On the Preference of Some Freshwater Plants in Finland for Brackish Water

By E. STEEMANN NIELSEN

Several freshwater species—both animals and plants—may be found in brackish water. Among the flowering plants belonging to the freshwater species going out into brackish water *Myriophyllum spicatum* can be mentioned. The distribution in Denmark of this species clearly shows that it is a freshwater species but able to go out into brackish water to about 7–8 ‰ S (IVERSEN, 1934).

It has, however, been shown by LINDBERG (1911) and LUTHER (1951), that *Myriophyllum spicatum* in Finland is found nearly exclusively in brackish water. A series of other freshwater plants has the same distribution in Finland. Some of them may occasionally be found in freshwater but their main distribution is along the coast of the Baltic. According to the admirable treatise by LUTHER, 1951, the group consists of the following species:

<i>Potamogeton filiformis</i>	<i>Ranunculus confervoides</i>	<i>Nitellopsis obtusa</i>
<i>P. pectinatus</i>	<i>Callitriche autumnalis</i>	<i>Chara tomentosa</i>
<i>P. panormitanus</i>	<i>Myriophyllum spicatum</i>	<i>Chara aspera</i>
<i>Zannichellia repens</i>	<i>Utricularia neglecta</i>	
<i>Najas marina</i>		

The preference which the above mentioned species show for brackish water in Finland is of course not due to the salinity. This is e. g. very clearly pointed out by LUTHER who, further, is of the opinion that: “die Innengrenzen der Arten dieser Gruppe durch Aussüßung des Brackwassers mit den Arten nicht zusagendem fennoskandischem Urgesteinswasser bedingt zu sein scheinen.”

As all the species in question are found in nature only in alkaline waters (cp. IVERSEN, 1929) it is obvious to think of pH being the factor de-

termining the distribution of the species. By studying the distribution in the brackish water of the Ekenäs-Region in Southern Finland, LUTHER, however, was able to show convincingly that pH cannot be of major importance for the distribution. The water of the whole region investigated was found to be alkaline showing only slight variations from place to place. According to BUCH (1914) pH varies between 7.1 and 7.9 in the region. Freshwater localities not influenced by brackish water were not visited during the investigations in question.

LUTHER also makes it clear that the total content of electrolytes cannot be of major importance for the distribution of the species in the brackish water of the Ekenäs-Region. Thus why the less saline waters of the Baltic, diluted by the inflow of rivers from the Fennoscandian bed-rock, should be an unsuitable habitat for the plant species mentioned above, LUTHER leaves an open question.

An important factor governing the distribution of aquatic plants has, however, been overlooked by LUTHER, as it has been by nearly all other investigators dealing with the distribution of freshwater plants, viz. the carbon source for photosynthesis. LUTHER (1951) p. 33 writes: "Da der Kohlensäuregehalt der Oberflächenschichten mit der atmosphärischen Kohlensäure im Gleichgewicht steht dürfte genügend  $\text{CO}_2$  den höheren Wasserpflanzen überall zur Verfügung stehen". Dissolved carbon dioxide in equilibrium with the carbon dioxide of the air should, according to this, be sufficient for the photosynthesis of the flowering plants having submerged leaves. Experimental work has, however, showed that this statement is far from being correct. The rate of photosynthesis in *Myriophyllum spicatum* at 0.015 millimols free  $\text{CO}_2/\text{L}$ , which is the concentration of  $\text{CO}_2$  in water in equilibrium with the atmosphere at  $15^\circ \text{C}$ . ( $\text{CO}_2$  tension 0.03 per cent.), is negligible according to STEEMANN NIELSEN (1947), Fig. 3. A concentration of free  $\text{CO}_2$  10 times as high is necessary in order to produce a rate of photosynthesis 50 per cent. of the maximum rate if no other carbon source is available. At a  $\text{CO}_2$  tension of 0.03 per cent. the rate of photosynthesis, with regard to the free  $\text{CO}_2$ , is thus nearly without any importance at all in aquatic plants like *Myriophyllum spicatum*, whereas the leaves of the terrestrial plants at this  $\text{CO}_2$  tension have a rather vigorous rate of photosynthesis.

In the leaves of the terrestrial plants  $\text{CO}_2$  is diffused through the stomata and the intercellular spaces to the cells in which the photosynthesis is going on. As this diffusion takes place in a gas, it occurs at a high rate. Only when the  $\text{CO}_2$  molecules diffuse through the thin cell walls to the chloroplasts found immediately inside the walls, have they

to diffuse dissolved in water. Such a diffusion takes place at a rate of quite a different and smaller order of magnitude. The insignificant thickness of the layer—about one  $\mu$ —prevents the slow rate of diffusion from being of any decisive importance.

Conditions are different in the aquatic (submerged) plants where there are often layers of quite a different order of magnitude across which the  $\text{CO}_2$  has to diffuse dissolved in water. In *Myriophyllum spicatum* the maximum thickness of this layer is about  $40\mu$  (the distance of the farthest chloroplast from the surface). The rate of diffusion is inversely proportional to the distance.

Growth experiments with *Helodea canadensis* and *Ceratophyllum demersum* have rendered similar results as the experiments on photosynthesis—STEEMANN NIELSEN (1944). Nearly no growth at all was found if free  $\text{CO}_2$  in equilibrium with the  $\text{CO}_2$  of the atmosphere was the only carbon source.

There exists, however, another carbon source for autotrophic aquatic plants. Species like *Myriophyllum spicatum*—but not all aquatic plants—are able to utilize  $\text{HCO}_3^-$  ions directly in photosynthesis. RUTTNER (1921) was the first to show that aquatic plants can utilize  $\text{HCO}_3^-$  in photosynthesis although he was of the opinion that free  $\text{CO}_2$  is the absolutely most important carbon source. ARENS (1936) showed that  $\text{OH}^-$  ions were released from the upper side of the leaves of aquatic plants when  $\text{HCO}_3^-$  ions were used as the carbon source for the photosynthesis. The quantitative side of the photosynthesis by means of  $\text{HCO}_3^-$  ions was worked out by STEEMANN NIELSEN (1947) who showed that this carbon source is actually the most important one in a lot of aquatic plants. A concentration of about 1 milliequiv.  $\text{HCO}_3^-$  per litre is necessary in *Myriophyllum spicatum* in order to establish a rate of photosynthesis 50 per cent of the maximum rate if  $\text{HCO}_3^-$  is the only carbon source—STEEMANN NIELSEN (1947), Fig. 5 and Fig. 18. In the alkaline Danish waters where this species lives, a concentration of  $\text{HCO}_3^-$  of at least this size is found. In oceanic seawater a concentration of about 2 milliequivalents/L is found.

The fresh water which is carried out by the Finnish rivers into the Baltic has only a rather insignificant content of  $\text{HCO}_3^-$ . The alkalinity (Titration alkalinity) of the Finnish rivers flowing into the Bottniska Viken is according to BUCH (1944) in average 0.30 milliequiv./L. The concentration of  $\text{HCO}_3^-$  may in this water be put equal to the titration alkalinity. At a concentration of 0.30 milliequiv.  $\text{HCO}_3^-$  per litre the rate of photosynthesis in *Myriophyllum spicatum* is only about 15 per cent. of the maximum rate. It is thus quite clear why the species is not able to live



in this water unless it has been mixed with brackish water from the Baltic having a higher content of  $\text{HCO}_3^-$ .

The alkalinity in Bottniska Viken is according to BUCH (1945)  $= 0.16 + 0.358 \cdot \text{Cl } \text{‰}$  ( $\text{Cl } \text{‰} = 0.555 \cdot \text{S } \text{‰}$ ). As the alkalinity of the water of the Swedish rivers flowing into the Bottniska Viken, according to BUCH, in average is the same as the alkalinity of the Finnish rivers ( $= 0.30$ ) it could have been imagined that the invariable in the equation given above should have been 0.30 instead of 0.16. A discussion about the reasons for the deviation in question may be seen in BUCH (1945), p. 98. Here attention should be called to the fact, that the titration method used for the determination of the alkalinity of the freshwater samples was rather rough. The values from freshwater are in fact not comparable with the exact measurements of the brackish water.

1 milliequiv.  $\text{HCO}_3^-$  per litre is according to the equation above found at a salinity of  $4.2 \text{ ‰}$ , 0.5 milliequiv. per litre at  $1.7 \text{ ‰}$  S, 0.3 milliequiv. per litre at  $0.7 \text{ ‰}$  S. According to Fig. 18 in STEEMANN NIELSEN (1947) the rate of photosynthesis at a concentration of 0.5 milliequiv.  $\text{HCO}_3^-$  per litre was 30 per cent. of the maximum rate, at 0.3 milliequiv./L it was 15 per cent. It is, however, not possible at present to make out where the lower limit in the concentration of  $\text{HCO}_3^-$  is most likely to be found in *Myriophyllum* growing in nature. There are several complications to take into account.  $\text{HCO}_3^-$  ions do not represent the only carbon source. Although free  $\text{CO}_2$  is mostly only of minor importance in the photosynthesis of *Myriophyllum spicatum* under natural conditions, local enrichment of free  $\text{CO}_2$  because of decaying organic matter may increase importance of this carbon source.

In the photosynthetic experiments with *Myriophyllum* mentioned above, specimens which originated from a lake showing a high concentration of  $\text{HCO}_3^-$  (between 2 and 3 milliequiv. per litre) were used. We do not know at present if specimens from a locality showing a much lower concentration of  $\text{HCO}_3^-$  behave in just the same way. If the anatomy of the leaves is somewhat different—the distance of the chloroplasts from the surface being on the average shorter—the specimens will most likely be able to grow at a lower concentration of  $\text{HCO}_3^-$  than the specimens in the experiments mentioned above.

It is thus premature to explain in detail the distribution in Finland of *Myriophyllum spicatum*—and the other species behaving principally in the same way in relation to salinity. It would, however, be of considerable interest to make experiments showing the dependence of the photosynthetic rate on the concentration of  $\text{HCO}_3^-$  and free  $\text{CO}_2$  using

specimens of the different species from localities near the inner boundaries of their distribution in a Finnish coastal area.

LUTHER (1951), p. 105, points out that several of the freshwater species in Finland found only in brackish water—e. g. *Potamogeton pectinatus*—at the inner boundaries of their distribution prefer localities exposed to the action of the waves, whereas the same species at higher salinities are able to grow in places where the sea is always calm. When making experiments in aquatic plants showing the dependence of the rate of photosynthesis on the concentration of the different carbon sources, the importance of constantly stirring the experimental water has been shown. Fig. 4 and Fig. 7, STEEMANN NIELSEN (1947) show that the rate of photosynthesis (real assimilation) in *Myriophyllum* is significantly reduced at lower concentrations of  $\text{HCO}_3^-$  if the experimental water is not stirred. At 0.3 milliequiv.  $\text{HCO}_3^-$  per litre (7000 lux) the rate in stagnant water was found to be reduced to about  $1/6$  compared with the rate in water being constantly stirred. If the concentration of the carbon source is low in nature, flowing water or the action of waves may thus in many aquatic plants be of decisive importance for the rate of photosynthesis.

### Summary.

An explanation is given of the fact shown e. g. by LUTHER, 1951, that several species of freshwater plants in Finland are found nearly exclusively in brackish water. It is shown that a sufficient concentration of  $\text{HCO}_3^-$ —the main carbon source in the photosynthesis of these species—in Finland normally only occurs in brackish water, the alkalinity of the water of the rivers here being to low. The preference of these species at the inner boundaries of their distribution for localities influenced by the action of waves is also explained.

### References.

- ARENS, K., 1936: Physiologisch polarisierter Massenaustausch und Photosynthese bei submersen Wasserpflanzen. II. Die  $\text{Ca} (\text{HCO}_3)_2$ -Assimilation. — J. wiss. Bot. 83: 513.
- IVERSEN, J., 1929: Studien über pH-Verhältnisse dänischer Gewässer und ihren Einfluss auf die Hydrophyten-Vegetation. — Bot. Tidsskr. 40: 277.
- 1934: Studier over Vegetationen i Ringkøbing Fjord før Hvide Sande-Kanalens Aabning 1931. in JOHANSEN, A. C. & BLEGVAD, H.: Ringkøbing Fjords Naturhistorie i Brakvandsperioden 1915–1931, p. 18. København 1933–36.

- LUTHER, H., 1951: Verbreitung und Ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Südfinnland. I. Allgemeiner Teil. – *Acta Botanica Fennica* 49: 1.
- RUTTNER, F., 1921: Das elektrolytische Leitvermögen verdünnter Lösungen unter dem Einfluss submerser Gewächse. – *Sitzungsber. Akad. d. Wissensch. in Wien. Mathem.-naturw. Klasse*, 130.
- STEEMANN NIELSEN, E., 1944: Dependence of Freshwater Plants on Quantity of Carbon Dioxide and Hydrogen Ion Concentration. Illustrated through Experimental Investigations. – *Dansk Bot. Arkiv*, 11, 8.
- 1947: Photosynthesis of Aquatic Plants with special Reference to the Carbon-Sources. – *Ibidem* 12, 8.
- 1951: The Marine Vegetation of the Isefjord. – *Medd. Komm. Danmarks Fisk.- og Havunders. Serie: Plankton*, 5, 4.

Some New Observations Concerning the  
Geographic Distribution and the Ecology of *Arenaria*  
*humifusa* WG. in Norway as Compared with  
*Arenaria norvegica* GUNN.

By ROLF NORDHAGEN

It is a well known fact that many plant species do not thrive in closed communities, viz. among other plants, but always prefer more or less open habitats or new soil. Some of the very best examples are the shrub *Myricaria germanica* and the perennial herb *Silene tatarica*. From Switzerland several authors have described a series of open or half-open vegetation types, calling them associations because of the lawfulness of their floristic composition. The plants concerned are termed "Schuttpflanzen", a designation which is not easily translated into other languages. In English the words debris, scree(s), talus, and gravel are often applied to the habitats in question. I myself have sometimes used the jocular term "vagabond plants" about the species concerned, but this designation is not an adequate one as a good many unsocial plant-species are very rare and appear to be absolutely non-expansive, at any rate in the present age.

To this ecological category rather many arctic-alpine species belong, in Northernmost Norway for instance *Arenaria humifusa*, *A. norvegica*, *A. ciliata* \**pseudofrigida*, *Braya linearis*, *B. purpurascens*, *Erigeron politum*, *Minuartia rubella*, *Papaver Dahliaenum*, *P. lapponicum*, and *P. radiculatum*.

The bulk of these species are ecologically exacting in so far as they decidedly prefer or even demand a basic or subneutral soil rich in electrolytes. I shall here only go into detail with regard to *Arenaria humifusa* WAHLENBERG, which was described from a Swedish mountain by this prominent botanist in 1812, then confused with *Arenaria norvegica* GUNNERUS until 1934, when it was rediscovered in Northern Norway by

the present author. In the sequel I am, however, also going to discuss the ecological difference between the said two species.

Since 1935 when I wrote my treatise on the taxonomy, the ecology and distribution of *Arenaria humifusa* (NORDHAGEN, 1936a), I have found it in some new places on Mageröy and in one single place on the north-western side of Söröy in Western Finmark (cp. NORDHAGEN, 1936b). The plant has also been rediscovered by NILS DAHLBECK in 1940 on the locus classicus Mount Tuki (= Lill-Tokin, WAHLENBERG, 1807, 1812; cp. SELANDER, 1943, 1950). An old find from Mandalen on the Lyngenfjord in Troms made by E. JÖRGENSEN (1894) has come to light during the arrangement of his bryological collections after his death. JÖRGENSEN used the name *Arenaria norvegica* GUNN. var. *humifusa* (WG.).

In spite of the fact that *Arenaria humifusa* on the mountain Duksfjell southeast of North Cape grows together with *Arenaria norvegica*, the ecology of these two species is different. Visiting Mageröy again in 1936, I came across *A. humifusa* not far from the village Honningsvaag in the lowlands on intensely disintegrated gabbro and only 10 m. above sea-level. The summer had been a very hot one, and the soil consequently had dried up, but according to information from a man living in the neighbourhood, the locality is usually "boggy" (Fig. 1). It displayed traces of frost upheaval and solifluction. In two different places I analysed a quadrat per 4 m<sup>2</sup>. and in the table below I have put the results side by side with the notes which I published from Duksfjell in 1936. The numbers in the 8 first columns indicate the "Deckungsgrad" according to the scale of HULT-SERNANDER.

A third and fourth occurrence were found by me in 1936 on a small peninsula lying between Skibsfjord and Kamöyvaer, likewise on the eastern side of Mageröy, in the vicinity of the small Skibsfjord Lakes ca. 25–30 m. above sea-level, near a rivulet on moist, boggy terraces influenced by slight solifluction. The accompanying species here were about the same as near Honningsvaag (*Betula nana*, *Cerastium cerastoides*, *Loiseleuria* (sterile), *Pinguicula alpina* & *vulgaris*, *Sagina intermedia*, *Salix reticulata*, *Scirpus caespitosus*, *Selaginella selaginoides*, *Silene acaulis*, *Thalictrum alpinum*, and *Tofieldia pusilla*).

Being convinced that the big island Söröy in Western Finmark had displayed ice-free refuges during the last ice-age, at any rate along its northwestern side, I went by steamer to Galten on Söröy the 19th of July 1936 and, having hired a small motorvessel, began to hunt for *Arenaria humifusa* on the promontories or small but majestic peninsulas which here face the ocean over a stretch of ca. 50 km. (NORDHAGEN 1940). But I





Fig. 1. Habitat of *Arenaria humifusa* WG. near Honningsvaag on Magerøy at an elevation of ca. 10 m. Boggy flat of disintegrated gabbro with tufts of *Scirpus caespitosus* \**austriacus* (cp. analysis in text). August 1936. (NORDHAGEN phot.).

did not find it. The sixth day, however, when having followed the boat from Galten "inland" to Sanden near Veidnes in the Dønnesfjord and climbed the hills straight west of the nice houses at Veidnes (these were like the rest of the houses on Sörøy burnt down by enemies during the war 1940–1945), I got my reward. At an elevation of 140 m. on flattish ground, consisting of disintegrated mica-schists with some quartz and being covered by a wind-cut *Dryas octopetala*-*Carex rupestris*-*Carex glacialis*-stand, I found an area of about 50 m<sup>2</sup>. which appeared to have suffered from regelation or frost upheaval in winter and spring. In fact parts of it were destitute of any vegetation; but in a corner, facing the South-West, where the naked soil had a brownish tint, I came across a very limited number of tiny specimens of *Arenaria humifusa*. A few of them were pressed and are now incorporated in the herbarium of the University of Bergen. An analysis (4 m<sup>2</sup>.) of the vegetation from this "corner" is found in the table as column no. 6. Setting aside the absence of *Arenaria norvegica*, which at Veidnes occurred a couple of hundred meters farther to the North in dry limestone screes, the accordance between this quadrat analysis from Sörøy and the five from Duksfjell on

Table 1. Patches with *Arenaria humifusa*  
on Mageröy (I, III), Söröy (II) and Mount Tuki in Lule Lappmark (IV).

Localities:	I					II	III		IV	
Quadrats: 4 m <sup>2</sup> (except no. 9-10)	1	2	3	4	5	6	7	8	9	10
<i>Arenaria humifusa</i> . . . . .	+	1	+	+	+	1	2	2	×	.
— <i>norvegica</i> . . . . .	1	1	1	1	1	—	—	—	—	—
<i>Bartsia alpina</i> . . . . .	—	—	—	—	—	+	—	—	—	—
<i>Campanula rotundifolia</i> . . . . .	—	—	—	—	—	—	—	—	—	—
<i>Cerastium alpinum</i> . . . . .	1	+	—	+	1	—	1	—	—	—
<i>Chamorchis alpina</i> . . . . .	—	1	—	—	1	+	—	—	—	—
<i>Cochlearia officinalis</i> . . . . .	—	—	—	—	—	—	1	1	—	—
<i>Equisetum variegatum</i> . . . . .	1	1	—	—	1	—	1	1	—	—
<i>Euphrasia frigida</i> . . . . .	—	+	+	—	+	1	1	+	—	—
<i>Minuartia rubella</i> . . . . .	—	—	—	—	—	—	—	—	—	—
<i>Pinguicula alpina</i> . . . . .	1	1	1	1	1	—	1	1	—	—
— <i>vulgaris</i> . . . . .	—	—	—	—	—	—	1	1	—	—
<i>Polygonum viviparum</i> . . . . .	1	1	1	1	2	+	1	1	—	.
<i>Potentilla Crantzii</i> . . . . .	—	—	—	—	—	—	—	—	×	—
— <i>nivea</i> . . . . .	—	—	—	—	—	—	—	—	×	—
<i>Rumex acetosa</i> . . . . .	—	—	—	—	—	—	2	1	—	—
<i>Sagina caespitosa</i> . . . . .	—	—	—	—	—	—	—	—	(.)	(.)
— <i>intermedia</i> . . . . .	—	—	—	—	—	—	1	1	—	—
— <i>saginoides</i> . . . . .	—	—	—	—	—	—	1	1	—	—
— <i>nodosa</i> . . . . .	—	—	—	—	—	—	1	1	—	—
<i>Saxifraga aizoides</i> . . . . .	—	—	1	—	+	1	1	1	—	—
— <i>nivalis</i> . . . . .	—	—	—	1	—	—	—	—	—	—
— <i>oppositifolia</i> . . . . .	1	1	1	1	2	1	—	—	(×)	(×)
<i>Selaginella selaginoides</i> . . . . .	1	—	1	1	—	—	1	1	×	—
<i>Silene acaulis</i> . . . . .	2	2	1	3	2	2	2	3	(×)	(×)
<i>Thalictrum alpinum</i> . . . . .	2	2	2	1	1	2	1	1	×	—
<i>Tofieldia pusilla</i> . . . . .	1	1	1	1	1	—	1	1	(×)	(×)
<i>Viola biflora</i> . . . . .	+	+	—	—	—	—	—	—	—	—
<i>Carex Bigelowii</i> . . . . .	1	1	1	1	1	1	1	1	—	>
— <i>capillaris</i> . . . . .	—	—	1	2	1	—	1	2	(×)	(×)
— <i>glacialis</i> . . . . .	1	—	—	—	—	2	—	—	×	—
— <i>rupestris</i> . . . . .	2	1	2	2	2	1	—	—	×	.
<i>Deschampsia alpina</i> . . . . .	—	—	—	—	—	—	1	1	—	—
<i>Festuca ovina</i> . . . . .	1	1	1	2	1	+	1	1	—	×
— <i>rubra</i> . . . . .	—	—	—	—	—	—	1	1	—	—
<i>Juncus biglumis</i> . . . . .	—	—	—	—	—	+	—	—	—	—
— <i>trifidus</i> . . . . .	1	—	1	—	—	—	—	—	—	—
— <i>triglumis</i> . . . . .	—	—	—	—	—	—	1	2	—	—
<i>Luzula spicata</i> . . . . .	—	—	—	—	—	—	1	—	—	—
<i>Poa alpina</i> . . . . .	—	—	—	—	—	—	1	1	—	—

Table 1 (continued.)

Localities:	I					II	III		IV	
Quadrats: 4 m <sup>2</sup> (except no. 9-10)	1	2	3	4	5	6	7	8	9	10
<i>Scirpus caespitosus</i>										
<i>*austriacus</i> . . . . .	—	—	—	—	—	—	2	2	—	—
<i>Betula nana</i> (low) . . . . .	—	—	—	—	—	—	1	1	—	—
<i>Dryas octopetala</i> . . . . .	2	1	3	1	2	2	—	—	—	—
<i>Empetrum hermaphroditum</i> .	1	1	—	1	—	1	1	—	—	—
<i>Salix myrsinites</i> (low) . . . .	—	—	1	—	—	—	1	1	—	—
<i>polaris</i> . . . . .	—	—	—	—	—	—	—	—	—	—
— <i>reticulata</i> . . . . .	2	2	1	1	1	1	—	—	( )	( )
<i>Vaccinium uliginosum</i> . . . .	—	1	—	—	—	—	1	1	—	—
<i>Cetraria nivalis</i> . . . . .	—	—	—	—	—	—	—	—	—	—
<i>Campylium stellatum</i> . . . .	—	—	—	—	—	—	2	2	—	—
<i>Drepanocladus intermedius</i> .	—	—	—	—	—	—	1	1	—	—
<i>Webera</i> sp. . . . .	—	—	—	—	—	—	1	1	—	—
<i>Polytrichum juniperinum</i> . .	—	—	—	—	—	—	—	—	—	—
<i>Nostoc</i> sp. . . . .	—	—	—	—	—	—	3	3	—	—
Naked gravel, stones . . . . .	4	4	4	4	4	4	4	4	?	?
Vascular plants . . . . .	20	20	19	18	20	18	30	27	(8)	(8)

Mageröy is astounding. In the columns no. 9 and 10 I have put together the botanical facts which SELANDER (1950, II, p. 81) has published about the locus classicus in Lule Lappmark. He describes the very limited habitat (ca. 50 m<sup>2</sup>.) as a somewhat moist and gravelly area influenced by frost upheaval and lying upon slates at the south-western foot of Mount Tuki. The floristic accordance with the Norwegian habitats is good.

The quadrats no. 7 and 8 from Honningsvaag on Mageröy, however, differ from the others by displaying a more hygrophilous flora (cp. *Sagina intermedia*, *Sagina nodosa*, *Deschampsia alpina*, *Juncus triglumis*, *Scirpus caespitosus*, *Campylium stellatum*, and *Drepanocladus intermedius*) whereas *Dryas cotopetala*, *Carex glacialis*, and *C. rupestris* are lacking.

Summing up my experience as to the ecology of *Arenaria humifusa* in Scandinavia, I would characterize the species as seasonal hygrophilous and subneutrophilous (cp. the pH-value 6.8 from Duksfjell). It appears to be wholly incapable of forming closed mats in spite of both subterranean runners (cp. NORDHAGEN, 1936a, Figs. 2 and 3) and good seed production, and it never enters closed communities.

Ecologically it comes rather near to *Sagina caespitosa*, which however seems to be still more hygrophilous and decidedly more chionophilous (cp. NORDHAGEN, 1954, p. 12–16).

It is regrettable that no concrete items of information concerning the ecology of this interesting species are available from West Greenland, North America, and its isolated habitat on Spitzbergen (POLUNIN, 1943), setting aside general descriptions in handbooks. Both its rareness and its peculiar ecology in Northern Scandinavia point in the direction that the species now-a-days is a relict, having had its last “golden age” during the lateglacial, that is: before closed plant-communities came into existence.

That *Arenaria humifusa* earlier has been overlooked because of its smallness, is seen from the many new North American records which MARCEL RAYMOND has brought to light. In Scandinavia, however, many localities which appear appropriate to it, have been searched by botanists during the last 20 years; but as far as I know not a single new find has turned up since 1936. In Sweden the locus classicus from 1807 is still unrivalled, and the country of LINNÆUS and WAHLENBERG without doubt belongs to the best explored on earth. The map Fig. 2 shows the known distribution of *Arenaria humifusa* in Scandinavia.<sup>1)</sup> A map of its total geographic area has been prepared by Dr. RAYMOND and the author with a view to the future editing of the “Encyclopædia Arctica”.

After the publication of WAHLENBERG's Flora lapponica (1812) *Arenaria humifusa* became confounded with *A. norvegica* GUNN. The chief cause of this confusion was the mixed collection of the said two species which ÅNGSTRÖM, 1837, brought back from Mount Tuki, and the smallness of his *humifusa*-specimens compared with those of *norvegica*. Scandinavian botanists after WAHLENBERG seem to have regarded the *humifusa*-specimens simply as depauperated modifications of *norvegica*; but as I have shown in 1936, *A. humifusa* is a very distinct species, both its vegetative system and its flowers (corolla, capsule, seeds) being different from those of *A. norvegica* and *A. ciliata* \**pseudofrigida*.

Ecologically there is a certain accordance between these three taxa in so far as they belong to the category “unsocial plants”. But *A. humifusa* is by far the faintest of them. In Table no. 2 below I have grouped

<sup>1)</sup> The map published by HULTÉN, 1950, has got an erroneous dot in Finmark (southeast of the Island Seiland, between Komagfjord and Lærrisfjord; the herbarium specimens from this area are *Arenaria norvegica*).



Fig. 2. The geographic distribution of *Arenaria humifusa* Wg. in Scandinavia.

(F = Rybatchi or the Fisher Peninsula, now Russian territory; here *A. humifusa* has been found by Finnish botanists in three places).



vegetation analyses from four different localities in Northern Norway where *Arenaria norvegica* gave the impression of having optimal life-conditions. In three of them it was accompanied by *Braya linearis*, another "vagabond plant" (Fig. 4), which, however, is more exacting than the said *Arenaria*-species in so far as it nearly always keeps to limestone, dolomite or calciferous mica-schists whereas *A. norvegica* is met with also on pure mica-schists and phyllites. In the table I have primarily put down analyses of 10 quadrats per 4 m<sup>2</sup>. from the very interesting screes on the southwestern side of the mountain Baatfjell in Junkerdal in the province Nordland, ca. 60°50' N., at an elevation of about 700 m. (Fig. 3). These whitish screes are due to the steep precipice above, which causes unfailing avalanches in winter and spring. The soil was not absolutely dry during my visit; I got the impression that some feeble veins of ground water were oozing through the upper part of the screes, and this was perhaps the reason why *Dryas octopetala* occurred only as small, stray individuals. At a lower level the slopes had much more of it. The foot of all these screes was covered by luxuriant *Betula*-forests and *Salix*-thickets with tall herbs and grasses; but one could see how the avalanches had spoiled certain stripes of forest.

The columns no. 13–15 (series nr. IV) refer to a smaller scree lying under the mountain Tausa northeast of Baatfjell at an elevation of 1050 m. Here *Braya linearis* was lacking, but *Minuartia rubella*, another typically unsocial plant-species, and three *Draba*-species were present.

Similar constellations of species are met with in Finmark. Unfortunately I have no quadrat analyses from this area, but in the columns no. 11 and 12 I have inserted two species lists from dry limestone screes on the northwestern side of Söröy. The first one from Russefjell near Veidnes in Dönnestjord at an elevation of 90 m. is facing the South. It was extremely dry during my visit the 30th of July 1930. On both sides of the scree I found very beautiful *Dryas*-heaths. In 1936 I visited the locality again and found the scree nearly as dry as in 1930, the *Braya*-plants being veritable dwarfs. The second scree is situated near Ytre Böle in Bölefjord and consists of decomposed mica-schists mixed with fragments of marble. At an elevation of only 15 m. *Arenaria norvegica* was rather frequent, whereas *Braya linearis* was scarce. The slope was facing the East and extremely dry.

From Lule Lappmark SELANDER (1950, II, p. 91–92) describes the typical habitats of *Braya linearis* as "calciferous screes", and the species lists published by him show a striking coincidence with my Table no. 2. Otherwise this contains the bulk of the typical "vagabond plants" belong-



Fig. 3. The screes at the foot of the south-western precipices of Baatfjell, Junkerdal in the province Nordland. *Arenaria norvegica* GUNN. and *Braya linearis* ROUY are both frequent on the gravel. August 1933. (NORDHAGEN phot.).

ing to the arctic-alpine element of the flora of Northern Scandinavia except the *Papaver*-species of the group *Scapiflora*. In Southern Norway *Artemisia norvegica* and *Cardaminopsis petraea* can be added to the list, whereas *Braya linearis* here is restricted to the screes of one single mountain, where curiously enough *Arenaria norvegica* is absolutely lacking (cp. map by NORDHAGEN, 1936a; unfortunately this important occurrence of *Braya* has escaped the attention of HULTÉN, 1950).

The fine gravel in the upper parts of the screes under Baatfjell showed the pH-value 8.18 (NORDHAGEN, 1936, cp. 71). According to my opinion such open communities as these form an ecological parallel to the alliance *Thlaspeion rotundifolii* of the Middle European "Kalkschuttgesellschaften" (BRAUN-BLANQUET, 1926; JENNY-LIPS, 1930). I have called



Fig. 4. *Braya linearis* ROUY growing in a limestone scree on the south-western side of Baatfjell, Junkerdal in Nordland, ca.  $66^{\circ}50'$  N. August 1933. (NORDHAGEN phot.).



Fig. 5. Disintegrated surface of dolomite on Biggallæfjell, Inner Baasfjord, Varanger Peninsula in Finmark. On the gravel *Arenaria ciliata* subsp. *pseudofrigida* OSTENF. & DAHL is frequent. August 1936. (NORDHAGEN phot.).



Table 2. Scree vegetation on limestone and mica-schists with *Arenaria norvegica* GUNN. and *Braya linearis* ROUY in Northern Norway.

I = Baatfjell, Junkerdal (Nordland). II–III = list of species from limestone screes near Veidnes and Ytre Bøle on Söröy (Finmark). IV = Tausafjell, Junkerdal (Nordland). The numbers in the columns 1–10 and 13–15 give the “Deckungsgrad” of the species according to the HULT-SERNANDER method.

Localities:	I										II	III	IV		
Quadrats (4 m <sup>2</sup> ) or stands:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Arenaria norvegica</i> .....	1	1	1	1	1	2	1	2	1	1	×	×	2	2	2
<i>Braya linearis</i> .....	1	2	2	1	2	1	1	1	1	1	×	×	—	—	—
<i>Minuartia rubella</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1
<i>Tussilago farfara</i> .....	1	—	1	—	1	—	1	—	—	1	—	—	—	—	—
<i>Veronica fruticans</i> .....	—	1	—	—	—	—	1	—	1	1	—	×	—	—	1
<i>Agropyrum latiglume</i> .....	1	1	1	1	1	1	—	—	1	1	—	—	1	1	1
<i>Alchemilla alpina</i> .....	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
<i>Antennaria alpina</i> .....	—	—	—	—	—	1	1	—	—	1	—	—	—	—	—
— <i>dioeca</i> .....	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
<i>Arabis alpina</i> .....	1	—	1	1	1	1	2	1	1	—	—	—	1	1	1
— <i>hirsuta</i> .....	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—
<i>Astragalus alpinus</i> .....	1	1	—	—	1	—	1	1	1	1	—	—	1	1	1
<i>Campanula rotundifolia</i> ...	1	1	1	1	1	2	1	1	1	2	—	—	1	—	1
<i>Cerastium alpinum</i> .....	1	1	1	1	1	1	1	1	1	1	×	×	1	1	1
<i>Chamorchis alpina</i> .....	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—
<i>Draba alpina</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—
— <i>fladnizensis</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1
— <i>incana</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>rupestris</i> .....	—	—	—	1	—	—	1	1	—	—	—	—	1	1	1
<i>Epipactis atrorubens</i> .....	—	—	—	—	—	1	—	—	—	—	×	—	—	—	—
<i>Equisetum scirpoides</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Erigeron boreale</i> .....	—	—	—	1	—	—	—	—	1	—	×	—	—	—	—
— <i>uniflorum</i> .....	—	—	—	—	—	—	—	—	—	—	×	—	1	—	1
<i>Erysimum hieracifolium</i> ...	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—
<i>Euphrasia frigida</i> .....	1	—	—	—	1	—	1	—	1	—	—	—	—	—	—
<i>Gentiana aurea</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>nivalis</i> .....	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
<i>Gymnadenia conopsea</i> .....	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
<i>Hieracium</i> sp.....	1	1	—	—	1	1	1	1	1	1	—	—	—	—	—
<i>Leontodon autumnalis</i> .....	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—
<i>Minuartia stricta</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1
<i>Oxyria digyna</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Oxytropis lapponica</i> .....	—	—	—	1	—	1	—	1	—	1	—	—	1	1	1
<i>Parnassia palustris</i> .....	—	—	1	—	—	—	—	—	1	1	—	×	—	—	—
<i>Polygonum viviparum</i> .....	2	1	—	1	—	1	1	1	—	1	—	—	1	1	1
<i>Polystichum lonchitis</i> .....	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—

Table 2 (continued).

Localities:	I										II	III	IV		
Quadrats (4 m <sup>2</sup> ) or stands:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Potentilla Crantzii</i> .....	1	1	—	—	—	1	1	1	—	1	×	—	—	—	1
<i>Pyrola norvegica</i> .....	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
<i>Ranunculus acris</i> .....	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Rubus saxatilis</i> .....	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—
<i>Rumex acetosa</i> .....	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—
<i>Saussurea alpina</i> .....	—	—	—	1	—	1	—	—	—	—	×	—	1	—	—
<i>Saxifraga aizoides</i> .....	3	2	1	2	3	3	2	3	2	3	×	×	3	3	3
— <i>oppositifolia</i> ....	1	1	1	1	1	1	1	1	2	1	×	×	1	2	1
<i>Sedum acre</i> .....	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—
<i>Silene acaulis</i> .....	1	1	1	—	1	1	—	—	—	1	×	—	1	1	1
<i>Solidago virgaurea</i> .....	1	1	—	1	1	2	2	—	1	2	—	—	1	—	1
<i>Taraxacum</i> sp. ....	—	—	1	—	—	—	1	1	1	1	—	—	—	—	—
<i>Thalictrum alpinum</i> .....	1	—	—	—	—	—	—	1	—	1	×	—	—	—	1
<i>Viola biflora</i> .....	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Anthoxanthum alpinum</i> ....	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—
<i>Carex glacialis</i> .....	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
— <i>rupestris</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Festuca ovina</i> .....	1	1	—	1	—	1	1	1	1	1	—	—	1	1	1
— <i>rubra</i> .....	—	—	—	—	—	—	—	—	1	—	×	×	—	—	1
— <i>vivipara</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Poa alpina</i> .....	1	1	1	—	1	1	1	1	1	1	×	—	1	1	1
— <i>glauca</i> .....	1	1	1	1	1	1	1	1	—	1	×	×	—	1	1
— <i>nemoralis</i> .....	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Trisetum spicatum</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1
<i>Betula tortuosa</i> (juv.) .....	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—
<i>Dryas octopetala</i> .....	—	—	—	1	—	—	—	1	1	1	×	×	1	1	1
<i>Salix arbuscula</i> .....	1	1	—	1	1	1	—	1	1	—	—	—	—	—	—
— <i>hastata</i> .....	—	—	—	—	—	1	—	1	—	—	—	—	—	1	1
— <i>lanata</i> .....	—	1	—	—	—	1	—	—	1	—	—	—	—	—	1
— <i>myrsinites</i> .....	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
— <i>reticulata</i> .....	—	—	1	—	—	—	—	—	1	1	×	—	1	1	1
Vascular plants .....	22	19	15	18	18	23	23	24	24	30	(30)	(15)	24	24	29

the Scandinavian group *Arenarion norvegicae* (NORDHAGEN, 1936c), but much work has still to be done before the floristical and ecological relation between this group and other scree communities, for instance those described by me from the Sikilsdal (NORDHAGEN, 1943), is sufficiently cleared up.

From Greenland and Arctic North America very little appears to have



been written about the ecology of *Braya linearis* and *B. glabella*. A comparison between its behaviour on both sides of the North Atlantic is therefore impracticable at present.

If we now return to *Arenaria humifusa* and compare the Tables no. 1 and 2, the floristic relationship between all the analysed quadrats is evident (of the 48 vascular plants in Table no. 1 nearly 46% are found in Table no. 2; of the 67 species in Table no. 2 nearly 33% are present in Table no. 1). But the difference is also easily perceptible: *Arenaria humifusa* is accompanied by *Equisetum variegatum*, *Pinguicula alpina*, *P. vulgaris*, *Selaginella selaginoides*, *Tofieldia pusilla*, *Carex capillaris*, in certain habitats also by *Sagina intermedia*, *S. saginoides*, *S. nodosa*, *Deschampsia alpina*, *Juncus triglumis*, *Scirpus \*austriacus*, and hygrophilous mosses absolutely lacking in Table no. 2. Reversely *Arenaria norvegica* is accompanied by *Veronica fruticans*, *Agropyrum latiglume*, *Arabis alpina*, *Astragalus alpinus*, *Oxytropis lapponica*, *Solidago virgaurea*, *Poa glauca*, and several other species which until now never have been found together with *A. humifusa*. Altogether the screes where *A. norvegica* seems to thrive excellently, display a much more xerophilous flora or vegetation than the gravelly flats where *A. humifusa* has its ecological optimum. Whereas *A. norvegica* is able to persist in rather steep and unstable (but not too coarse) screes, the tiny and weak *A. humifusa* keeps to flattish ground where frost upheaval and slight solifluction prevent stronger plants from getting foothold.

It is indeed very difficult to detect *Arenaria humifusa* in nature, firstly because of its smallness, secondly because the individuals always are few and far between, and thirdly because the flowers never dehisce or expand their petals in the same way as in *A. norvegica* GUNN. and *A. ciliata \*pseudofrigida* OSTENF. & DAHL. An intimate knowledge of its ecology is therefore necessary to all botanists who intend searching for it in future.

The ecology of *Arenaria ciliata \*pseudofrigida* OSTENF. & DAHL appears to be consistent with that of *A. norvegica*. In July 1936 I visited one of its chief haunts in Finmark viz. the inner Baasfjord district. Near the lake Persvatnet ca. 150 m. above sealevel I saw plenty of it growing on disintegrated dolomites and slates, mostly in a flat or faintly sloping situation (Fig. 5). Here it formed beautiful small mats upon the gravel, and I got the impression that upheaval of the soil by frost did not harm it, in fact some of the most vigorous specimens occurred on areas influenced by regelation. In August 1939 I paid a second visit to Baasfjord in order to make satisfactory analyses of the typical habitats, but a

pelting rain made it impossible to take notes in the open. The following list, however, gives a rather representative picture of the floristic milieu of *\*pseudofrigida* on the Varanger Peninsula: *Dryas octopetala*, *Bartsia alpina*, *Campanula rotundifolia*, *Cerastium alpinum* var. *lanatum*, *Chamorchis alpina*, *Potentilla Crantzii*, *Saxifraga oppositifolia*, *Silene acaulis*, *Carex rupestris*, *Festuca ovina*, *Tofieldia pusilla*, *Vaccinium uliginosum*, and *V. vitis-idaea*. On the south-western side of Baasfjord I found lots of *\*pseudofrigida* growing on disintegrated and very dry dolomite ledges together with *Asplenium viride*, *Carex glacialis*, *Chamorchis alpina*, *Erigeron politum*, *Polystichum lonchitis*, *Veronica fruticans*, and *Dryas octopetala*. Both in this district and on Syltefjord the *\*pseudofrigida* sometimes occur in wind-cut *Dryas*-heaths, but only as a subordinate component. In Western Finmark this is also the case with *Arenaria norvegica*. Both are very resistant to drought.

According to the cytological investigations made by amanuensis KRISTIAN HORN (cp. the preliminary publication in LÖVE & LÖVE, 1948) *A. norvegica* GUNN. has the chromosome number  $2n = 80$  whereas *A. ciliata* *\*pseudofrigida* OSTENF. & DAHL has  $2n = 40$ . In Northern Scandinavia up to its very northern and eastern limit (Mageröy and Porsangerfjord) *A. norvegica* fruits abundantly, in fact one finds loose seeds lying on nearly all herbarium sheets collected from the middle of July to the end of August. *A. ciliata* *\*pseudofrigida*, per contra, which is a much coarser and more conspicuous species, forming sometimes big mats, displays a very limited seed-production, in fact it is rather difficult to find ripe seeds in the capsules even in August, and this is also the case with the rather copious pressed material from Eastern Finmark preserved in the Oslo herbarium. According to the authors opinion *A. norvegica* GUNN. certainly is a species of its own, being restricted to Scandinavia, Iceland and Scotland, whereas *A. ciliata* *\*pseudofrigida* comes very near to the Middle-European *\*tenella* (KIT.) BRAUN-BLANQUET, which I had the opportunity to study in Switzerland (Engadin) in August 1953. The taxon *\*pseudofrigida* was only given the rank of a subspecies by OSTENFELD & DAHL, and in spite of the efforts made by some Russian and Scandinavian botanists during the last decades to raise its taxonomical rank, the view held by OSTENFELD & DAHL certainly is the correct one.

I hope to be able to return to these problems when having revised my *Arenaria*-collections from Ireland and Switzerland, and likewise to the interesting plant-geographical questions attaching each and all of the Scandinavian *Arenaria*-species of the *ciliata*-group (cp. NORDHAGEN, 1952).

## Postscript.

Since my article about *Arenaria humifusa* Wg. has gone to press, the Norwegian periodical "Nyt Magazin for Botanikk" Vol. 3, Oslo 1954, has appeared. In this volume the Swedish botanist OLOF RUNE has published a paper with the title "*Arenaria humifusa* on Serpentine in Scandinavia". Here DR. RUNE describes some new finds of the said species and gives an important new contribution to the ecology of this interesting species. Our two papers are thus completing each other.

## Literature.

- BRAUN-BLANQUET, JOSIAS, 1926: Vegetationsentwicklung und Bodenbildung in der alpinen Stufe der Zentralalpen. Unter Mitwirkung von Hans Jenny. Denkschr. d. Schweiz. Naturf. Gesellsch. 63. Zürich.
- HULTÉN, ERIC, 1950: Atlas of the Distribution of Vascular Plants in N.W. Europe. Stockholm.
- JENNY-LIPS, HANS, 1930: Vegetationsbedingungen und Pflanzengesellschaften auf Felsschutt. Beihefte zum Bot. Centralblatt 46. Dresden.
- JÖRGENSEN, EUGEN, 1899: Om floraen i Nord-Reisen og tilstødende dele af Lyngen. Christiania Vidensk. Selsk. Forhandl.
- LÖVE, ASKELL, and LÖVE, DORIS, 1948: Chromosome Numbers of Northern Plant Species. Reykjavik.
- NORDHAGEN, ROLF, 1936: Om *Arenaria humifusa* Wg. og dens betydning for utforskningen av Skandinavias eldste floraelement. Bergens Museums Aarbok 1935, Naturv. rekke nr. 1. Bergen.
- 1936b: Skandinavias fjellflora og dens relasjoner til den siste istid. Nordiska Naturforskarmötet i Helsingfors. Helsinki-Helsingfors.
- 1936c: Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens. Bergens Museums Aarbok 1936, Naturv. rekke nr. 7.
- 1940: Staurene ved Ofjordnæringen paa Söröya. Et eldgammelt strandnivaa i Vest-Finnmark. Summary: Stacks on Söröya in Western Finnmark. Indications of an inter-glacial or pre-glacial raised beach in Northern Norway. Norsk Geogr. Tidsskrift VIII, 1940. Oslo.
- 1943: Sikilsdalen og Norges fjellbeiter. En plantesociologisk monografi. Bergens Museums Skrifter nr. 22.
- 1952: *Arenaria*, in LAGERBERG, T., HOLMBOE, J. and NORDHAGEN, R.: Våre ville planter. Revidert og forøkt utgave. 2: 323–326. Oslo.
- 1954: Apologi for *Poa stricta* Lindeberg. Svensk Botanisk Tidsskrift.
- POLUNIN, NICHOLAS, 1943: Geographical Distribution of *Arenaria humifusa* Wahlenberg, New to the Flora of Spitzbergen. Nature.
- SELANDER, STEN, 1943: *Arenaria humifusa* och dess senaste öden i Sverige. Sveriges Natur.
- 1950: Floristic Phytogeography of South-Western Lule Lappmark I–II. Acta Phytogeographica Suecica No. 27–28. Uppsala.
- WAHLENBERG, GÖRAN, 1812: Flora lapponica. Berolini.

Hvilke betingelser må være opfyldte,  
for at *Helodea canadensis* kan opnå den optimale  
udvikling, der er årsag til dens massevis  
optræden i naturen?

Af CARSTEN OLSEN

Indledning.

*Helodea canadensis* er som bekendt en nordamerikansk vandplante, som i 1836 indførtes til Irland, hvorfra den siden har bredt sig over det meste af Europa. I Danmark iagttoges den første gang i 1870 i Søgård Sø i Sønderjylland, og den findes nu udbredt over det meste af landet. Indvandringen er dog ikke endt, idet den stadig indfinder sig i vandområder, hvor den ikke før har været iagttaget. Hvor betingelserne for dens trivsel er til stede, kan den i løbet af kort tid dække bunden i damme og vandløb, idet den i mange tilfælde fortrænger alle andre submerse vandplanter.

Det har længe været kendt, at *Helodea* for at opnå en frodig udvikling kræver forholdsvis kalkholdigt vand med neutral eller svag alkalisk reaktion. I Danmark forekommer den således kun i vand med pH-værdier fra 7.0–8.0 (IVERSEN, 1929, NYGAARD, 1938). Rigelig tilførsel af næringsstoffer, herunder også kuldioxyd og bikarbonat, er naturligvis også nødvendigt for, at planterne kan opnå en stor stofproduktion (STEEMANN-NIELSEN, 1944). Foretagne undersøgelser af forfatteren af nærværende afhandling tyder imidlertid på, at også andre betingelser må være opfyldte.

Grunden til, at disse undersøgelser blev foretaget, var den, at *Helodea* blev benyttet som forsøgsplante ved forsøg over ionoptagelse foretagne på Carlsberg Laboratoriet. Planterne blev hentet i en lille dam på Strødam, kaldet „Sorte Øje”, som er helt opfyldt af *Helodea*, der her opnår en ualmindelig kraftig udvikling. Da der over en længere periode var brug for rigeligt materiale af denne plante, besluttedes det at dyrke den i vandkultur for stadig at have nyt materiale til rådighed.

Planterne blev dyrket i cylindriske glasbeholdere, hver på 5 liter. Som næringsopløsning benyttedes almindeligt ledningsvand tilsat kaliumnitrat og fosfat samt mikronæringsstoffer, og ferricitrat anvendtes som jernkilde. En jævn strøm af atmosfærisk luft tilsat 5% kuldioxyd blev ledet gennem opløsningerne. Denne foranstaltning tjente dels til at forsyne planterne med kuldioxyd til brug ved fotosyntesen, dels til at modarbejde den pH-stigning i opløsningerne, som vandplanternes fotosyntese medfører. Opløsningernes pH-værdi varierede indenfor området 7.0–8.0.

*Helodea* trivedes imidlertid ikke i disse opløsninger, idet stofproduktionen var meget ringe. De oprindeligt indførte skuddele bevarede en tid deres normale grønne farve, men nytilvæksten og de fremkomne sideskud blev spinkle og antog en rødbrun farvetone, og efterhånden ophørte al yderligere tilvækst. Planternes udseende tydede på vanskeligheder med hensyn til jernforsyningen, idet bladene på de nye skud var yderst fattige på klorofyl. Den rødbrune farvetone skyldtes antocyandannelse i bladcellerne.

Opløsningernes pH-værdi lå mellem 7.0 og 8.0, altså indenfor det område, der hersker i *Helodeas* naturlige voksemedium, men disse pH-værdier er højere end dem, man sædvanligt opretholder ved dyrkning af landplanter i vandkultur. Jernforsyningen er vanskeligere, jo højere opløsningens pH-værdi er, idet ferriionens opløselighed er ganske overordentlig ringe i opløsning med pH-værdi omkring 7.0. Ganske vist var jernkilden ferricitrat, hvori jernet er komplekst bundet og derfor ikke skulle udfældes af opløsningen, selv når denne har pH-værdier mellem 7.0 og 8.0. Men ferricitrat er meget ubestandigt og nedbrydes hurtigt. Ved vandkulturforsøg med landplanter må det derfor tilsættes med passende tidsmellemrum, når opløsningernes pH-værdi er høj. I stærkt lys udfældes jernet i ferricitrat derimod næsten øjeblikkeligt som ferrihydroxyd, og dette sker naturligvis også i *Helodea*-kulturerne, idet opløsningerne må stå i fuldt lys i modsætning til vandkulturer af landplanter, hvor opløsningerne befinder sig i mørke. Det var derfor ret sandsynligt, at *Helodea*-planterne ikke under de givne forsøgsbetingelser har kunnet forsyne sig tilstrækkeligt med jern.

#### Undersøgelser foretagne på *Helodea canadensis*' naturlige voksesteder.

Efter afslutningen af de mislykkede dyrkningsforsøg, besluttedes det at undersøge forholdene i nogle damme i Nordsjælland, i hvilke der findes en yppig vegetation af *Helodea canadensis*.



„Sorte Øje” på Strødam er en lille kredsrund dam ca. 15 m. i diameter, som er fuldstændig opfyldt af *Helodea*. Dammen, som er beskrevet af NYGAARD (1938), er omgivet af granskov, som nu er stærkt udhugget, så vandfladen ikke mere er så beskyttet, som den tidligere har været. Vandet er svagt gulligt og i tykkere lag ikke helt klart, men svagt opaliserende, antagelig som følge af et ringe indhold af ferrifosfat. På overfladen ses ofte små skumflager, som dannes, når luftbobler, som hidrører fra anaerobe processer i dyndbunden, stiger op til overfladen. Dybden er næppe noget sted over  $1\frac{1}{4}$  m. Planterne er rodfæstet i bunden og når helt op til overfladen, så at hele vandmassen er opfyldt af planterne, som blomstrer rigeligt sidst på sommeren. Bunden består af et tykt lag dynd. Dyndet er okkergult på overfladen, men under denne kulsort. Trækker man planterne forsigtigt op, følger de rodfæstede dele med, tilligemed et tykt lag sort dynd, som hænger ved rødderne.

Tæt ved „Sorte Øje” ligger den af bøgeskov omgivne 170 m lange Storedam, som også omtales hos NYGAARD (1938). I et ca. 5 m bredt bælte langs bredden skræner bunden, der her består af sand og grus uden dyndlag, svagt ud mod dammens midte, og i dette område findes *Helodea* ikke. Hele dammens midterparti har derimod dyndbund, som et tæt bevokset med en yppig vegetation af *Helodea*. Skønt dybden ikke er større end i „Sorte Øje”, når planterne ingen steder op til overfladen, de danner en tæt manke hen over bunden, men der er et frit vandlag på ca.  $\frac{1}{2}$  m eller mere ovenover planterne. Trækkes planterne op, ses også her det sorte dynd på rødderne.

Badstuedammen og Ødammen nord for Hillerød er ligesom de mange kanaler i „Indelukket” tæt bevokset med *Helodea*, og også her følger det sorte dynd med, når planterne trækkes op. Badstuedammen og Ødammen er iøvrigt flere gange med nogle års mellemrum midlertidigt blevet tørlagte og rensed op; sidste gang fjernede man det meste af dyndlaget, men efter at dammen påny var blevet fyldt med vand, indfandt *Helodea* sig allerede i den følgende sommer i betydelig mængde.

Endelig skal omtales en lille smal dam ved Furesø, som ligger tæt ved det sted, hvor kanalen mellem Lyngby Sø og Furesø løber ud i Furesøen. Dammen har oprindeligt været en lille vig fra Furesøen, men er nu adskilt fra denne. Vanddybden er ikke over 40 cm, og bunden er ler uden dyndlag. Her findes en tæt og meget yppig vegetation af *Helodea*, der ligesom i Storedammen på Strødam danner en tæt manke henover bunden, og der findes et frit vandlag på ca. 20 cm over planterne. Dammen ligger helt frit, og som følge af den lave vandstand, kan vandet om sommeren midt på dagen opvarmes til ca. 30°. Planterne blomstrer

rigeligt. Trækkes planterne op, ser man, at det ved rødderne hængende ler er mere eller mindre sortfarvet.

Dette, at *Helodea* er en rodfæstet vandplante, er et forhold, som ikke har været tilstrækkeligt påagtet ved undersøgelser over dens krav til voksemediet. Man har indskrænket sig til at undersøge vandet, dets kalkholdighed, indhold af næringsstoffer, pH-værdien, o.s.v., men ikke tænkt på bundens beskaffenhed. RAUNKJÆR (1899) gør derimod opmærksom på, at *Helodea* er en rodfæstet vandplante, der ynder temmelig roligt, ikke for dybt vand med dyndet bund. Denne iagttagelse bekræftes fuldt ud af de foretagne undersøgelser.

Spørgsmålet er nu, om bundens natur spiller en rolle for *Helodea*'s trivsel, og om det sorte dynd eller ler kan have nogen betydning for planternes ernæring – specielt deres jernforsyning.

Det sorte stof, som findes i bunden på alle de omtalte voksesteder, er ferrosulfid. Lader man dyndet henstå udsat for luftens ilt, antager overfladen meget hurtigt en okkergul farve, idet ferrosulfidet iltes til ferrihydroxyd. Ferrosulfidet dannes som følge af anaerobe processer i dyndet, hvor der hersker absolut iltmangel, idet sulfat reduceres til sulfid, og ferriforbindelser til ferroforbindelser.

En prøve af dyndet fra „Sorte Øje” blev anbragt i en glasflaske, som blev fyldt helt op med destilleret vand og lukket med en gummiprop, så luftens ilt ikke kunne få adgang. Flasken blev derefter rullet på et rulleapparat i 4 timer, og indholdet derefter filtreret. Det klare farveløse filtrat havde pH-værdien 7.0 og viste sig at indeholde 5 mg jern pr. liter. Det er ca. 1000 gange mere jern, end der kan være i opløsning i en vandkultur med pH 7.0, når et ferrisalt anvendes som jernkilde. Ferroionens opløselighed i opløsning med pH 7.0 er nemlig ca. 1000 gange større end ferriionens.

Det er således en nærliggende mulighed, at *Helodea* kan optage det for dens normale udvikling nødvendige jern som ferroioner gennem rødderne i dyndlaget. I dette hersker der som nævnt absolut iltmangel som følge af de anaerobe processer, der foregår her, og jernet findes som ferroforbindelser. I vandet, der står over bunden, kan ferroforbindelser ikke eksistere, da vandet er iltrigt og yderligere iltes om dagen af den ved *Helodea*'s fotosyntese udskilte ilt. Her kan kun eksistere ferriforbindelser, men deres opløselighed er som nævnt så ringe, at de næppe kan have nogen betydning for planternes jernoptagelse. En jernoptagelse fra vandet gennem blade og stængler kan derimod finde sted, såfremt vandet indeholder komplekst bundet jern. Jern kan danne komplekse, opløselige forbindelser med visse humusstoffer, og sådanne komplekse

jernforbindelser findes netop i vandet fra „Sorte Øje“, der som nævnt er svagt gulligfarvet. Vandet, hvis pH-værdi er ca. 7.0–7.4, viste sig nemlig at indeholde 1 mg jern pr. liter. I Storedam fandtes i vandet kun 0.05 mg jern pr. liter, i dammen ved Furesøen 0.005 mg. I vandet i Storedam findes altså en ganske ringe mængde komplext bundet jern, nemlig ca.  $\frac{1}{20}$  af hvad der findes i „Sorte Øje“. I dammen ved Furesøen findes komplext bundet jern overhovedet ikke.

### Dyrkningsforsøg med *Helodea canadensis*.

Tilbage stod nu ved forsøg at konstatere rigtigheden af de ovenfor opstillede hypoteser om *Helodea*'s jernforsyning i naturen. Planterne blev dyrkede i cylindriske glasbeholdere på 5 liter i opløsninger med henholdsvis ferricitrat (forsøg 1), ferriversenat<sup>1)</sup> (forsøg 2), og ferrihumat (forsøg 3) som jernkilde. Desuden opstilledes tre forsøg, i hvilke der anbragtes et gruslag på 5 cm i bunden af beholderne. I det første af disse (forsøg 4) bestod bundlaget af rent Robbedalegrus, i det andet (forsøg 5) anbragtes under gruset et lag af dyndet fra „Sorte Øje“, og i det tredje (forsøg 6) et lag ferrosulfid blandet med grus.

Opløsningernes sammensætning var – bortset fra jernkilden – den samme i alle forsøgene. Der anvendtes til hvert forsøg – med undtagelse af forsøg 3 –  $2\frac{1}{2}$  liter Københavns ledningsvand tilsat samme mængde glasdestilleret vand, hvilket giver et indhold af ca. 50 mg calcium og 5 mg magnium pr. liter. Omtrent samme calcium- og magniumindhold findes i vandet fra „Sorte Øje“, som anvendtes i forsøg 3. Til alle opløsningerne, også til vandet fra „Sorte Øje“, tilsattes kaliumnitrat og primært kaliumfosfat, således at koncentrationerne blev henholdsvis 17 mg K, 25 mg  $\text{NO}_3$ , og 4 mg  $\text{PO}_4$  pr. liter. Desuden tilføjedes alle opløsningerne: 0,25 mg  $\text{MnSO}_4$ , 4  $\text{H}_2\text{O}$  – 0,20 mg  $\text{H}_3\text{BO}_3$  – 0,10 mg  $\text{ZnSO}_4$ , 7  $\text{H}_2\text{O}$  og 0,05 mg  $\text{CuSO}_4$ , 5  $\text{H}_2\text{O}$  pr. liter. I forsøg 1 og 4 tilsattes ferricitrat (2 mg Fe pr. liter) og i forsøg 2 ferriversenat (2 mg Fe pr. liter) som jernkilde. I forsøg 3 fandtes jernet i forvejen som naturlig forekommende

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<sup>1)</sup> „Versene“ er et amerikansk handelsnavn for æthylen-diamin-tetraeddikesyre, et stof som danner opløselige komplekser med mange metalioner, også med ferriioner. Ferriversenat er første gang og med udmærket resultat anvendt som jernkilde for forskellige landplanter i vandkultur af JACOBSON (1951); senere har WARIS (1952) ligeledes med udmærket resultat anvendt det som jernkilde for Desmediaceer. Ferriversenatopløsningen, som anvendtes i det ovenfor beskrevne forsøg 2, blev fremstillet efter JACOBSONS angivelse..

jernhumusforbindelse (1 mg Fe pr. liter). I forsøg 5 og 6 sattes ikke jern til opløsningen, idet dette her fandtes som ferrosulfid i bunden.

Et foreløbigt forsøg havde vist det formålstjenlige i at indføre så lille en plantemasse som muligt i de enkelte beholdere, idet det naturligvis er ønskeligt, at den under forsøget producerede tørstofmængde er stor i forhold til den oprindeligt indførte tørstofmængde. Der blev derfor i hver beholder ved forsøgets begyndelse indført 10 *Helodea*-skudspidser hver på ca. 5 cm længde. Dette gav en tørstofmængde på ca.  $\frac{1}{4}$  g pr. beholder. I de beholdere, hvor der var bund, blev den nederste halvdel af skudspidserne stukket ned i gruset. I de beholdere, hvor der ikke var bund, blev de anbragt frit svævende i opløsningen.

Forsøgene varede 27 døgn. Der blev anvendt kunstig belysning (lystofrør), og lyset blev kun slukket 4 timer hver nat. Om dagen modtog planterne, der henstod i et væksthuse, naturligvis også dagslys, og da tidspunktet for forsøgenes gennemførelse var slutningen af august og begyndelsen af september, var dette lys ikke ubetydeligt. For at sikre planternes fotosyntese, blev der stadig ledet en svag strøm af atmosfærisk luft, tilsat 5% kuldioxyd, gennem opløsningerne. pH-værdien kunne svinge fra 7,0–8,0, men lå mest omkring 7,4. Kalium, nitrat og fosfat-indholdet i opløsningerne blev stadig kontrolleret, og hver gang koncentrationen var kendelig aftaget, blev den bragt op til den oprindelige koncentration. Hen på slutningen af forsøgene begyndte alger at blive generende, og det blev nødvendigt at skifte opløsningerne flere gange. Ved forsøgets slutning blev planterne taget op, skyllet, tørret, og vejjet. Resultaterne af forsøgene ses i tabel 1. Tallene for tørstoftilvæksten er anført for neden. Disse tal repræsenterer altså tørstofmængden ved forsøgets slutning ÷ den oprindelige indførte tørstofmængde, som var ca.  $\frac{1}{4}$  g pr. beholder.

Det fremgår af tabellen, at væksten i forsøg 1, hvor jernkilden var ferricitrat, var stærkt hemmet, idet skudspidserne efterhånden antog en rødbrun farve, samtidig med at væksten gik i stå. Tilsidst fik alle bladene større eller mindre brune sortrandede pletter.

Ganske anderledes forholdt planterne sig i forsøg 2 og 3, hvor der som jernkilde var anvendt mere stabile, komplekse jernforbindelser. Her var væksten, som det ses af tørstoftilvæksten, overordentlig kraftig. Skuddene blev lange og forgrenede, og planterne havde normal grøn farve. Versenatplanterne i forsøg 2 havde en større stofproduktion og en mørkere grøn farve end nogen af de andre planter. *Helodea* kan altså dyrkes i vandkultur uden bund, når der blot som jernkilde anvendes en passende stabil kompleks jernforbindelse. Vandet fra „Sorte Øje” indeholder en sådan



Tabel 1.

Forsøg nr.....	1	2	3	4	5	6
Bund .....	ingen	ingen	ingen	grus	dynd	ferro-sulfid
Fe-kilde.....	ferri-citrat	ferri-versenat	ferri-humat	ferri-citrat	ferro-sulfid	ferro-sulfid
Skuddenes farve.	rød-brun	normal grøn	normal grøn	rød-brun	normal grøn	normal grøn
Tørstoftilvækst, g	0,36	1,90	1,81	0,40	1,02	1,25

komplex jernhumusforbindelse, som er en udmærket jernkilde for *Helodea*, og at det er denne forbindelses tilstedeværelse, der er årsag til, at tørstofproduktionen i forsøg 3 er 5 gange så stor som i forsøg 1 og ikke eventuelt andre forekommende stoffer i vandet fra „Sorte Øje” fremgår deraf, at tilsætning af jernversenat har ganske den samme virkning.

Forsøgene med bund (4–6) viste, at *Helodea* ikke trives, hvor bunden er rent grus, og hvor jernkilden er ferricitrat. Nytilvæksten fik brunrøde skudspidser, og væksten gik efterhånden i stå. Planterne trivedes lige så dårligt som i forsøg 1, hvor opløsningen havde samme sammensætning, og hvor jernkilden ligeledes var ferricitrat. Den eneste forskel var grusbunden, og denne har altså ingen indflydelse på planternes vækst.

Hvor der, som i forsøg 5, derimod fandtes et sort dyndlag under gruset fortsætter planterne væksten, og de nye skuddele får normal grøn farve. Det samme er tilfældet i forsøg 6, hvor dyndet er erstattet med ferrosulfid, og tørstoftilvæksten er i dette forsøg ovenikøbet større end i forsøget med dyndbund. Det forhold, at ferrosulfid har samme virkning som det naturlige dynd, viser altså, at det er ferrosulfidet i dyndet, der er årsag til planternes gode udvikling og normale grønne farve og ikke eventuelle andre stoffer i dyndet. Ferrosulfid kan altså benyttes som jernkilde, idet der ikke var tilsat nogen anden.

Ved forsøgets slutning viste det sig, at planterne i forsøg 5 og 6 havde talrige rødder nede i bunden. Disse rødder var alle udstyret med lange rodhår, og de fandtes i hele rodens udstrækning, der var altså ikke nogen begrænset rodhårzone. I den rene grusbund i forsøg 4 var der derimod kun få rødder.

Når det tidligere ikke lykkedes at dyrke *Helodea* i opløsninger med



relativ høj pH-værdi, skyldtes dette altså vanskeligheder med hensyn til planternes jernforsyning. De foretagne forsøg viste tydeligt, at det var jernforsyningen, der bestemte tørstofproduktionens størrelse, thi hvor denne ikke opnåede sin maximale værdi, var mangel på jern den begrænsende faktor.

### *Helodea's jernforsyning i naturen.*

Vanskeligheder med hensyn til *Helodea's* jernoptagelse gør sig naturligvis også gældende i naturen. Kun hvor vandet indeholder opløselige jernhumusforbindelser, eller hvor planterne har adgang til at optage jernet gennem rødderne fra en bund, hvori der hersker iltmangel, så at jernet findes som ferroforbindelser, kan *Helodea* opnå sin normale udvikling og heraf betingede betydelige stofproduktion.

I Storedam på Strødam findes kun en yderst ringe mængde komplext bundet jern, og i dammen ved Furesøen overhovedet intet. I disse to damme må *Helodea* være henvist til at dække sit jernforbrug ved at optage ferroioner fra bunden. Begge steder danner planterne, som tidligere nævnt på grund af *Helodea's* særlige voksemåde (nedliggende, rodslående skud), en forholdsvis kort, men tæt manke hen over bunden. Manken kan danne et 20-30 cm tykt lag, og over den befinder der sig åbent vand. Antagelig kan planterne i disse to damme og på mange andre lokaliteter, hvor der kun findes ganske lidt eller intet tilgængeligt jern i vandet, ikke fjerne sig alt for langt fra bunden, fra hvilken de må optage jernet som ferroioner, fordi de næppe kan transportere jernet over længere strækninger gennem stænglerne. At jernet undertiden fældes ud som ferrifosfat under transport i ledningsbanerne kan iagttages hos visse planter, bl. a. hos majs i vandkultur, og majsen bliver som følge heraf klorotisk. Udfældningen skyldes bl. a. for stort fosfatindhold og for høj pH-værdi i saften i karrene. Hos *Helodea* må transport over længere strækninger desuden vanskeliggøres, fordi stænglerne ikke besidder egentlige ledningsstrænge. Ledningsvævet er i hvert tilfælde meget stærkt reduceret.

I „Sorte Øje” på Strødam danner planterne derimod ikke nogen manke hen over bunden. Her er hele dammen opfyldt af planterne lige til overfladen. Kun i det øverste vandlag har skuddene grønne blade. I de underliggende lag er bladene enten gule eller endog helt forsvundne, fordi lyset udelukkes af den overliggende plantemasse. De friske *Helodea*-skud, som ligger nær overfladen, måtte have jernet tilført over en lang strækning,

Tabel 2.

cm fra skudspidsen	mg Fe pr. 1 g tørstof	
	Sorte Øje	Storedam
0- 5.....	1,28	0,40
5-15.....	1,20	1,05
15-25.....	1,25	1,40
25-35.....	1,38	2,60

hvis dette skulle optages fra bunden, og mange af skuddene har endog næppe forbindelse med denne. Men i „Sorte Øje” optager planterne sikkert ikke jernet fra bunden, men fra vandet, idet dette indeholder rigeligt af en kompleks jernhumusforbindelse.

At det virkelig forholder sig således, fremgår af det i tabel 2 viste forsøgsresultat. Bestemmer man jernindholdet i forskellige afsnit af *Helodea*-skuddene fra skudspidsen og nedefter indtil 35 cm's afstand fra spidsen, finder man nogenlunde samme jernindhold i de forskellige dele af skuddene, når disse er taget fra „Sorte Øje”, medens skuddene fra Storedam tydeligt viser aftagende jernindhold i retning mod spidsen, de yderste 5 cm af skuddene indeholder kun ca.  $\frac{1}{3}$  af den jernmængde, der findes i de tilsvarende skuddele fra „Sorte Øje”.

I „Sorte Øje” kan enhver del af skuddet optage jern direkte fra vandet; i Storedam optages det fra bunden og må ledes op gennem stænglerne til skudspidsen, men der mistes en del på vejen.

Forekomsten af komplekse jernhumusforbindelser i vandet i „Sorte Øje” er formodentlig betinget af omgivelsernes natur. Dammen ligger forholdsvis dybt, omgivet af granskov, hvis stærkt humusholdige bund skråner ned mod vandfladen, og den sandede og grusede undergrund indeholder betydelige mængder jern. I Sortedam nord for Hillerød, der også er en lille, dybtliggende skovdam, har jeg for en årrække siden fundet et jernindhold på 1 mg pr. liter. I denne stærkt beskyggede dam fandtes *Helodea* ikke, men vandfladen var tæt bedækket med *Lemna polyrrhiza*. Komplekse jernhumusforbindelser kan sikkert kun forekomme i større mængde i små skovdamme, og kun på sådanne lokaliteter kan *Helodea* dække sit jernforbrug ved optagelse af komplekst bundet jern fra vandet. I langt de fleste af de vandområder, hvor *Helodea* forekommer, er den derimod henvist til at dække sit forbrug af jern ved optagelse af ferroioner fra bunden.

Iøvrigt kan også andre planter end vandplanter optage jern som ferroion. I stiv lerjord kan der, navnlig når jorden er gennemvåd, let

opstå delvis iltmangel, hvorved ferroioner kan dannes. Planter, der vokser på lerbund, indeholder derfor som regel mere jern end de samme arter gør, når de vokser på sandbund. Men navnlig sumpplanter indeholder meget jern, som de optager som ferroioner fra dyndbunden. En plante som ris, der som bekendt er en sumpplante, bliver næsten altid klorotisk i vandkultur. Dens naturlige jernkilde er ferroionerne, som findes i dyndbunden, men dem kan man vanskeligt tilføre planterne i vandkultur. Her ville jernversenat sikkert vise sig at være en udmærket jernkilde.

### Summary.

#### What are the Conditions of Optimum Development Enabling *Helodea canadensis* to Grow Profusely in Nature?

Water culture experiments with *Helodea canadensis* showed that the plants did not develop normally in ordinary nutrient media containing ferric citrate as the source of iron. The apices of the shoots turned brown, and the leaves which developed during the experiments were very poor in chlorophyll. Eventually growth ceased. The appearance of the plants suggested difficulties with respect to iron nutrition.

Investigation of the natural habitat of *Helodea* (certain ponds in Northern Zealand) showed that wherever *Helodea* developed vigorously with a normal green color, the bottom of the pond was covered by a black layer of mud containing ferrous sulfide. The *Helodea* plants had numerous roots penetrating this mud layer. The presence of ferrous compounds is made possible by the anaerobic conditions prevailing. In water solution at pH 7.0, the solubility of ferrous ion is about 1000 times that of ferric ion. A sample of black mud from one of the ponds was placed in a glass bottle, which was then completely filled with distilled water and closed with a glass stopper excluding atmospheric oxygen. The bottle was mechanically rotated for four hours. Afterwards the contents were filtered. The filtrate had a pH value of 7.0 and contained 5 mg. Fe per liter.

This makes it plausible that *Helodea* can absorb a quantity of iron sufficient for normal development through its roots in the mud layer. In most of the localities studied the plants form a dense growth on the bottom, but do not reach the surface. Above them there is about 0.5 m. of water. In one pond only ("Sorte Øje") do the plants reach the surface, and here many of the plants are not rooted in the bottom. Their lower parts are more or less wilted because the mass of plants above them screens off light. In this pond the plants probably do not absorb iron from the bottom through their roots, but absorb it from the water through their leaves and stems. The water has a faint yellow color and contains a complex iron-humus compound (1 mg. Fe per liter). In the other ponds the water is colorless and contains no complex iron compounds in solution.

Renewed water culture experiments supported the above assumptions as to how *Helodea* obtains iron in Nature. Ferric citrate, which is decomposed by light, proved unsuited as an iron source, just as it did in the first experiments (Table 1, Experiment 1). More stable complex iron compounds proved better suited. This is

true of ferric versenate<sup>1)</sup> (Experiment 2) and of the iron humate from the pond mentioned. Water from this pond was used for the nutrient solution employed in experiment 3. The plants in experiment 1 grew reddish-brown, and their production of dry matter was slight. The plants in experiments 2 and 3 assumed a strong green color, and their production of dry matter amounted to around five times that encountered in experiment 1. Furthermore, experiment 5 showed the *Helodea* could develop normally with a strong green color in water cultures containing no complex iron compounds in solution, provided that each vessel contained a layer of gravel with an underlying layer of black ferrous sulfide-containing mud from one of the ponds where *Helodea* grew. The plants sent numerous roots into the mud. The mud layer could be replaced by a layer of pure ferrous sulfide mixed with gravel (Experiment 6), but if the bottom layer consisted solely of gravel (Experiment 4) the plants did not grow even if the nutrient solution contained ferric citrate as a source of iron.

This investigation shows that in Nature *Helodea canadensis* can only develop normally with considerable production of dry matter in localities where either the water contains soluble iron humates, or the plants have an opportunity to absorb iron from a bottom layer where oxygen is deficient so that the iron present is in the ferrous state.

### References – Litteraturliste.

- IVERSEN, J., 1929: Studien über die pH-Verhältnisse dänischer Gewässer und ihren Einfluss auf die Hydrophyten Vegetation. *Botanisk Tidsskrift* 40: 277.
- JACOBSON, L., 1951: Maintenance of iron supply in nutrient solutions by a single addition of ferric potassium ethylenediamine tetra-acetate. *Plant Physiology* 26: 411.
- NYGAARD, GUNNAR, 1938: Hydrobiologische Studien über dänische Teiche und Seen. *Archiv für Hydrobiologie* 32: 523.
- RAUNKJÆR, C., 1899: De danske Blomsterplanters Naturhistorie I. Enkimbladede. København.
- STEMANN NIELSEN, E., 1944: Dependence of freshwater plants on quantity of carbon dioxide and hydrogen ion concentration. *Dansk botanisk Arkiv* 11, nr. 8.
- WARIS, H., 1953: The significance for Algae of chelating substances in the nutrient solutions. *Physiologia Plantarum* 6: 538.

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<sup>1)</sup> Ethylene diamine tetra-acetic acid forms chelated complexes, especially with di- and trivalent ions. The iron complex employed in the experiments with *Helodea* was prepared in accordance with the directions of JACOBSON (1951).

## Sloping Mires in North-Western Norway

By HUGO OSVALD

In the northern part of Lofoten, on the island of Andoya, the large plains are covered in the main with bogs. These may be characterized as flat bogs (OSVALD, 1923, 1925a and b). But on higher levels—on the hills or low mountains—sloping mires are predominant. These may well be regarded as a combination of North-Scandinavian soligenous mires and the blanket bogs of Great Britain and Ireland. Undoubtedly, these mires are mainly fed by the heavy precipitation on the high levels, but there is also a conspicuous influence of water from mineral ground above the mires (OSVALD, 1925b). Remarkably, the vegetation of these mires displays a more southern character than the vegetation of the bogs on the lowland plains.

Similar mires, though less sloping, also occur in other parts of Lofoten. Together with the late Finnish botanist WIDAR BRENNER I had an opportunity to study such a mire on August 4, 1925.

This mire is located near Svolvær at the road to Kabelvåg, more exactly on the sloping ground between the small lake Kongens Vand and an adjacent hill.

The hill slope, which is comparatively steep, is covered by the birch forest characteristic of this region—a birch forest of heath type with *Vaccinium myrtillus* or *Empetrum nigrum* dominant in the field layer. The transition from this type of vegetation to the mire is represented by a birch forest rich in ferns; here the following species were noted:

*Athyrium filix-femina*

*Dryopteris austriaca*

– *dryopteris*

– *phegopteris*





Fig. 1. Profile through the sloping mire near Svolvaer. – 1. *Trichophorum austricum* – *Sphagnum papillosum* sociation. – 2. *Carex echinata* – *Sphagnum Girgensohnii* sociation. – 3. Birch forest rich in ferns. – 4. Birch forest of heath type.

Along the small streams traversing the area, the birch forest was rich in *Equisetum silvaticum*. A luxuriant liverwort was growing in the water, and *Sphagnum squarrosum* along the water course.

On the marginal part of the mire, bordering to the birch forest, the vegetation was the

*Carex echinata* – *Sphagnum Girgensohnii* sociation<sup>1)</sup>

from which the following note was made:<sup>2)</sup>

<i>Andromeda polifolia</i> .....	1	<i>Eriophorum angustifolium</i> .....	1
<i>Oxycoccus quadripetalus</i> .....	1	<i>Juncus filiformis</i> .....	1
<i>Comarum palustre</i> .....	1	<i>Molinia coerulea</i> .....	1
<i>Polygonum viviparum</i> .....	1	<i>Nardus stricta</i> .....	1
<i>Trientalis europaea</i> .....	1+	<i>Trichophorum caespitosum</i> subsp.	
<i>Viola palustris</i> .....	1	<i>austricum</i> <sup>3)</sup> .....	1
<i>Agrostis canina</i> .....	1	<i>Polytrichum commune</i> .....	1
<i>Carex brunnescens</i> .....	1	<i>Sphagnum Girgensohnii</i> .....	5
– <i>echinata</i> .....	3	– <i>parvifolium</i> .....	1
– <i>Goodenowii</i> .....	1	– <i>papillosum</i> .....	2
– <i>magellanica</i> .....	1	– <i>robustum</i> .....	1
– <i>pauciflora</i> .....	1		

<sup>1)</sup> A phytocoenose characterized by the dominant species in the name of the community (see DU RIETZ, 1936).

<sup>2)</sup> For the description of plant communities the HULT-SERNANDER method was employed using one square metre areas.

<sup>3)</sup> In the following referred to as *Trichophorum austriacum*.

Further out in the mire, where the water content of the peat is higher and the supply of mineral nutrients lower, the

*Eriophorum angustifolium* – *Sphagnum papillosum* sociation

is the dominant community. The following note may give an idea of its composition:

<i>Andromeda polifolia</i> . . . . .	1	<i>Trichophorum austriacum</i> . . . . .	1
<i>Viola palustris</i> . . . . .	1	<i>Calliergon stramineum</i> . . . . .	1
<i>Calamagrostis canescens</i> . . . . .	1—	<i>Sphagnum papillosum</i> . . . . .	5
<i>Carex pauciflora</i> . . . . .	2	— <i>apiculatum</i> . . . . .	4—
— <i>rariflora</i> . . . . .	1	— <i>Lindbergii</i> . . . . .	1
<i>Eriophorum angustifolium</i> . . . . .	4—	— <i>Warnstorffianum</i> . . . . .	1

In the same community the following species were found in addition:

<i>Vaccinium uliginosum</i> .	<i>Carex echinata</i> .
<i>Comarum palustre</i> .	— <i>magellanica</i> .
<i>Cornus suecica</i> .	<i>Nardus stricta</i> . <sup>1)</sup>

The more wet strips, where the water from the mineral ground soaks down over the mire, are characterized by the naked *Eriophorum angustifolium* sociation; between these soaks extends the community just described and the most important community of the mire, i. e. the

*Trichophorum austriacum* – *Sphagnum papillosum* sociation.

This community may be illustrated by two notes, one from this mire, *a*, and one made by DU RIETZ, Aug. 2, 1922, on another mire in the neighbourhood of Svolveaer (near Osan), *b*.

	<i>a</i>	<i>b</i>		<i>a</i>	<i>b</i>
<i>Andromeda polifolia</i> . . . . .	2	2	<i>Calypogeia trichomanis</i> . . . . .	—	1—
<i>Empetrum nigrum</i> . . . . .	1	1	<i>Cephalozia fluitans</i> . . . . .	1	1
<i>Oxycoccus microcarpus</i> . . . . .	1	1	— <i>sp.</i> . . . . .	1	1
<i>Cornus suecica</i> . . . . .	—	1+	<i>Jungermannia inflata</i> . . . . .	—	1
<i>Drosera longifolia</i> . . . . .	1	—	<i>Mylia anomala</i> . . . . .	1	—
— <i>rotundifolia</i> . . . . .	1+	1	<i>Riccardia latifrons</i> . . . . .	—	1
<i>Trientalis europaea</i> . . . . .	—	1	<i>Sphagnum fuscum</i> . . . . .	1	—
<i>Rubus chamaemorus</i> . . . . .	2	—	— <i>magellanicum</i> . . . . .	1	1
<i>Carex rariflora</i> . . . . .	1	—	— <i>papillosum</i> . . . . .	5	5
<i>Eriophorum vaginatum</i> . . . . .	1	—	— <i>plumulosum</i> . . . . .	—	1—
<i>Trichophorum austriacum</i> . . . . .	4	5—	— <i>rubellum</i> . . . . .	1	2
<i>Blepharozia ciliaris</i> . . . . .	1	1	— <i>tenellum</i> . . . . .	1	1
<i>Calliergon stramineum</i> . . . . .	1	1	— <i>Warnstorffianum</i> . . . . .	1	—

<sup>1)</sup> Sometimes developing into small patches of a *Nardus* community.

Some less important plant communities, for instance *Vaccinium uliginosum* – *Sphagnum parvifolium* sociation and *Empetrum nigrum* – *Sphagnum magellanicum* sociation, occur within the areas of those just described. In fairly dry parts of the mire, i. e. parts not influenced by water from mineral ground, also hummocks with *Calluna vulgaris* communities are to be found. These communities usually have a bottom layer of *Sphagnum fuscum*, in some cases also of *S. magellanicum* and *S. parvifolium*. A note from the

*Calluna vulgaris* – *Sphagnum fuscum* sociation

showed the following composition:

<i>Andromeda polifolia</i> . . . . .	1	<i>Pleurozium Schreberi</i> . . . . .	1
<i>Calluna vulgaris</i> . . . . .	4	<i>Rhytidiadelphus loreus</i> . . . . .	1
<i>Empetrum nigrum</i> . . . . .	1	<i>Calypogeia trichomanis</i> . . . . .	1
<i>Oxycoccus quadripetalus</i> . . . . .	1	<i>Cephalozia</i> sp. . . . .	1
<i>Vaccinium myrtillus</i> . . . . .	1	<i>Mylia anomala</i> . . . . .	1
– <i>uliginosum</i> . . . . .	1	<i>Sphagnum parvifolium</i> . . . . .	1
<i>Drosera rotundifolia</i> . . . . .	1	– <i>fuscum</i> . . . . .	5
<i>Pinguicula vulgaris</i> . . . . .	1	– <i>Girgensohnii</i> . . . . .	1
<i>Rubus chamaemorus</i> . . . . .	3	– <i>robustum</i> . . . . .	1—
<i>Carex magellanica</i> . . . . .	1	– <i>rubellum</i> . . . . .	1
<i>Eriophorum vaginatum</i> . . . . .	1		

In some places there were also *Trichophorum austriacum* – *Sphagnum tenellum* sociation and, in rather wet parts, *Trichophorum austriacum* – *Sphagnum Lindbergii* sociation.

The large area of mire west of the lake was dominated by the *Trichophorum austriacum* – *Sphagnum papillosum* sociation.

In addition the

*Trichophorum austriacum* – *Sphagnum tenellum* sociation

was noted here:

<i>Andromeda polifolia</i> . . . . .	1	<i>Sphagnum compactum</i> . . . . .	1
<i>Carex magellanica</i> . . . . .	1	– <i>Dusénii</i> . . . . .	1
<i>Drosera longifolia</i> . . . . .	1	– <i>Lindbergii</i> . . . . .	1
<i>Eriophorum angustifolium</i> . . . . .	1+	– <i>papillosum</i> . . . . .	1
<i>Trichophorum austriacum</i> . . . . .	4	– <i>tenellum</i> . . . . .	5

Another community of the smooth mire surface is the

*Eriophorum vaginatum* – *Sphagnum papillosum* sociation

which had the following composition:

<i>Andromeda polifolia</i> .....	1	<i>Carex pauciflora</i> .....	1
<i>Empetrum nigrum</i> .....	1	<i>Eriophorum vaginatum</i> .....	4
<i>Vaccinium uliginosum</i> .....	2	<i>Calliergon stramineum</i> .....	1
<i>Rubus chamaemorus</i> .....	1	<i>Sphagnum papillosum</i> .....	4
<i>Carex magellanica</i> .....	1	— sp. ....	3

Fairly dry parts of the mire were occupied by a naked

*Narthecium ossifragum* sociation,

which had the following composition:

<i>Calluna vulgaris</i> .....	1	<i>Molinia coerulea</i> .....	1
<i>Empetrum nigrum</i> .....	1	<i>Nardus stricta</i> .....	1
<i>Narthecium ossifragum</i> .....	5	<i>Trichophorum austriacum</i> .....	1
<i>Potentilla erecta</i> .....	2	<i>Psilidium ciliare</i> .....	1
<i>Rubus chamaemorus</i> .....	1	<i>Rhacomitrium lanuginosum</i> .....	1
<i>Trientalis europaea</i> .....	1	<i>Sphagnum papillosum</i> .....	1
<i>Viola palustris</i> .....	1	— <i>tenellum</i> .....	1
<i>Carex magellanica</i> .....	1		

Although the surface of the mire is conspicuously sloping it is mostly rather smooth. There are, however, areas where hummocks and hollows occur at right angle to the direction of the slope. In such areas the plant communities are arranged as indicated in Fig. 2.



Fig. 2. Arrangement of plant communities on areas with hummocks and hollows.

The *Trichophorum austriacum* – *Sphagnum compactum* sociation of this zonation has the following composition:

<i>Andromeda polifolia</i> .....	1	<i>Trichophorum austriacum</i> .....	4
<i>Drosera longifolia</i> .....	1	<i>Hepaticae</i> .....	1
— <i>rotundifolia</i> .....	1	<i>Sphagnum compactum</i> .....	5
<i>Eriophorum angustifolium</i> .....	1	— <i>Lindbergii</i> .....	1
<i>Molinia coerulea</i> .....	1	— <i>tenellum</i> .....	1

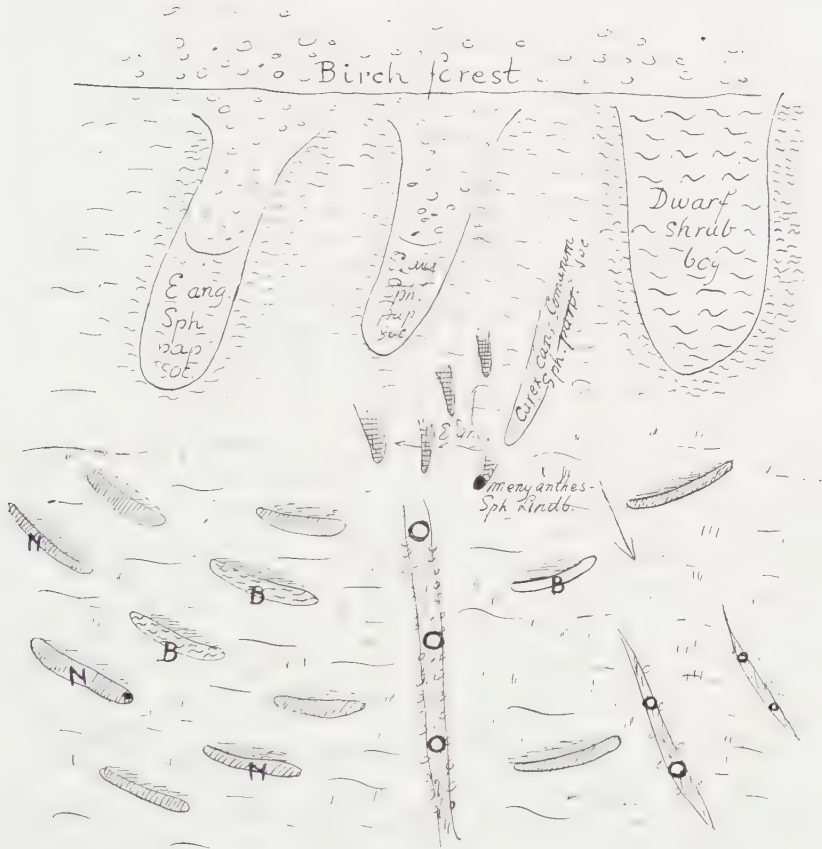


Fig. 3. Sketch of part of the sloping mire. - N = *Narthecium* hummocks. - B = Dwarf shrub hummocks. - O = Swallow holes.

Sometimes the differentiation between hummock and hollow is still more pronounced, for instance when the hollows are occupied by a naked *Eriophorum angustifolium* sociation and the adjacent hummocks by the *Narthecium ossifragum* sociation. Fig. 3 illustrates such an area.

On areas where the mire is not influenced by water from the mineral ground, small *Sphagnum* bogs develop which project into the *Trichophorum* mire. See Fig. 3. The vegetation of these "bogs" is composed of a number of dwarf shrub communities, for instance:

- Calluna vulgaris* - *Sphagnum fuscum* sociation.
- Calluna vulgaris* - *Sphagnum rubellum* sociation.
- Calluna vulgaris* - *Pleurozium Schreberi* sociation.
- Calluna vulgaris* - *Cladonia rangiferina* sociation.
- Empetrum nigrum* - *Sphagnum fuscum* sociation.
- Empetrum nigrum* - *Ptilidium ciliare* sociation.



Generally, these bogs are surrounded by an edge of the *Eriophorum vaginatum* – *Sphagnum papillosum* sociation.

From the middle of the upper margin of the mire, where the flow of water is evidently strongest, strips of fen soaks project into the mire; they are continued downwards by a stream soak with gallery wood, as has been indicated schematically in Fig. 3.

The stream soak is of the ordinary type, which has been described for instance from Komosse (OSVALD, 1923) and from the bogs on Andøya (OSVALD, 1925b). The stream is overgrown, except for a number of swallow holes, and bordered by birch forest rich in *Cornus suecica* and *Vaccinium myrtillus*, either naked or with a bottom layer of *Sphagnum Girgensohnii*.

According to DU RIETZ<sup>1)</sup>, most of the small mires in the neighbourhood of Lödingen (in Lofoten) are characterized in the first place by the *Trichophorum austriacum* – *Sphagnum papillosum* sociation, which is dominant on this mire. In addition, there are mires with naked *Trichophorum austriacum* sociation with bare peat between high tussocks of *Trichophorum*. Other fairly common communities on the Lödingen mires are *Calluna vulgaris* – *Sphagnum fuscum* sociations either rich in *Trichophorum* or in *Eriophorum vaginatum*, both of them with *Andromeda polifolia*, *Oxycoccus quadripetalus*, *Rubus chamaemorus*, and *Vaccinium myrtillus* in the field layer, and usually with some *Sphagnum magellanicum* and *S. rubellum* in the bottom layer.

To repeat, the mire now described may be regarded as a combination of the soligenous mixed mires of northern Scandinavia and the extreme oceanic bogs of the British Isles. The *Calluna vulgaris* – *Sphagnum fuscum* communities are very similar to those of the northern mixed mires, and the dominance of *Trichophorum austriacum* communities is another northern feature, while the *Nartheccium ossifragum* communities on areas not influenced by water from mineral ground remind one of plant communities of bogs in Ireland.

### Literature.

- DU RIETZ, G. E., 1936: Classification and Nomenclature of Vegetation Units. – Zesde International Botanisch Congres, Proceedings, Vol. II. Leiden.
- OSVALD, H., 1923: Die Vegetation des Hochmoores Komosse. – Sv. Växtsoc. Sällsk. Handl., 1.
- 1925a: Die Hochmoortypen Europas. – Festschrift Carl Schröter. Veröff. Geobot. Inst. Rübel in Zürich.
- 1925b: Zur Vegetation der ozeanischen Hochmoore in Norwegen. – Sv. Växtsoc. Sällsk. Handl., 7.

<sup>1)</sup> Personal communication.

## Electron Microscope Observations on *Codonosiga botrytis* (EHR.) JAMES-CLARK

By JOHS. BOYE PETERSEN and J. BENTH HANSEN

*Codonosiga* (*Codosiga*) *botrytis* (EHR.) JAMES-CLARK was erected by EHRENBURG under the genus *Epistylis* and referred to a new genus (*Codosiga*) by JAMES-CLARK (1866). Later, especially European, authors have used the form *Codonosiga* because it is derived from *κώδων*, a bell, and *αἴσιον*, be silent. The species is evidently very common in fresh water, but owing to its small size it has no doubt often been overlooked. The cell is described as colourless, globular or ovate, naked, 6–30  $\mu$  in diameter. At the anterior end there is a single flagellum, and around the base of this a plasmatic collar which is quite clear and transparent and which can be extended and withdrawn. When the cell is at rest the collar is infundibular; but it may suddenly contract and become conical, though with a distinct opening at the top. The lower part of the flagellum is rather immobile in the living condition, while the tip of it swings briskly, producing strong currents round the cell (KENT, 1880–82). The cell is attached to some object by means of a shorter or longer stalk, and on each stalk there may be several cells, just as the cells may in certain circumstances break away and swim around by themselves; in that case the flagellum points backwards. Propagation takes place by longitudinal division; a single author mentions transverse division (FRANCÉ, 1897). No sexuality has been demonstrated, even though STEIN (1878) thought he had seen copulation. FISCH (1885) observed the formation of cysts; germination occurred by the cyst membrane being ruptured and a number of small motile spores coming out, which at first had no collar. The nutrition is supposed to be holozoic and the chief food bacteria; but with respect to the consumption of food opinions have differed widely in the course of time, nor can this paper shed any light on the subject.

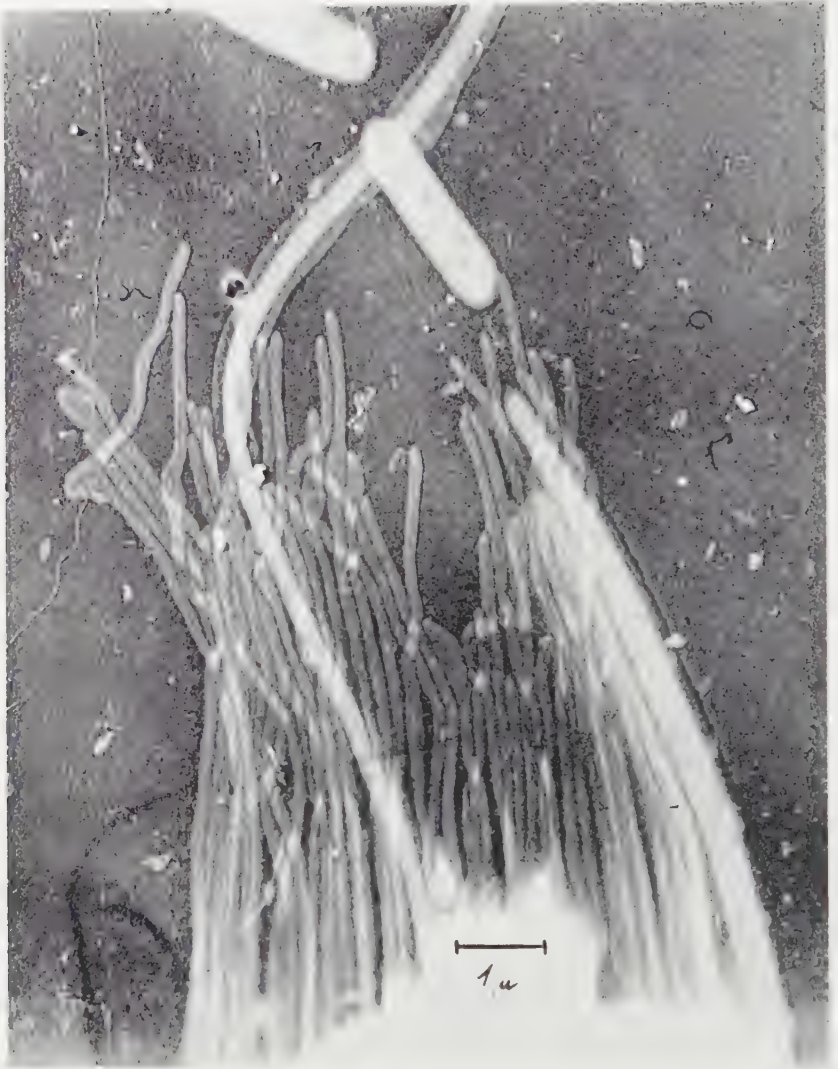


Fig. 1. The plasma collar, palladium shadowing after drying in the living state. A filamentous bacterium adhering accidentally to the tentacles. Initial enlargement 3600  $\times$ , total 10,000  $\times$ .

The material for the present investigation was procured by leaving water samples from divers localities to stand for some days in jars in the laboratory. A film was then formed on the surface, amongst other things of bacteria. To this film specimens of *Codonosiga* were very often found attached; it was then possible with a platinum loop to take



Fig. 2. Individual just divided. Vilh. Jensen's method.  
Initial enlargement 1600  $\times$ , total 3500  $\times$ .



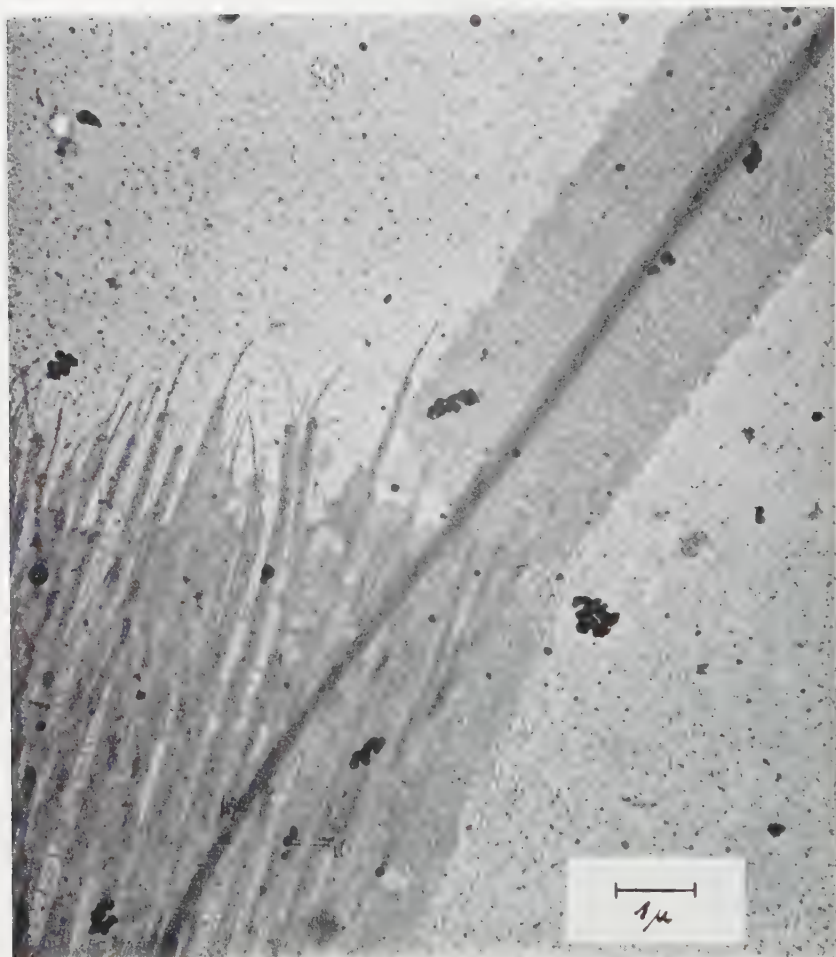


Fig. 3. Part of the left cell in fig. 2, more enlarged. The band along the flagellum can be seen down behind the tentacles, the structure seems to be like a network. Points of knobs forming faintly visible parallel lines. The fine appendages on the tentacles are supposed to be artefacts. Initial enlargement 3200  $\times$ , total 10,000  $\times$ .

a drop of the water containing some specimens of the species. Most of the samples were derived from the water-lily pond in front of the green-houses in the Botanical Garden, Copenhagen, and were collected in the autumn of 1953 and in January 1954.

For use at the electron micrography the material was fixed with osmic vapour and dried on formvar film with ensuing shadowing with palladium in the usual way. In other cases the material was fixed and dried on slides





Fig. 4. Two cells on a common stalk, the border only visible on one flagellum. Vilh. Jensen's method. Initial enlargement 650  $\times$ , total 2150  $\times$ .

and then treated in the following way: Subjected for 5 minutes during slight heating to mordanting with VILH. JENSEN's mordant (to 100 ml. of a solution of 10 p. c. tannic acid and 6 p. c. alum are added 40-60 ml. of ZIEHL's carbol fuchsine); after this thoroughly rinsed in water and stained with a saturated watery fuchsine solution with cautious heating for a short time. This gave a distinct staining of the flagella. With an object marker some of the best stained individuals were encircled and they were then transferred to the formvar film in the usual way by covering the slide with a collodium film which was stripped off and laid on the



Fig. 5. Part of Fig. 4 more enlarged. The more or less interwoven fibrillar structure is seen. The granules are crystals of the staining chemicals. Initial enlargement 3600  $\times$ , total 11,500  $\times$ .

formvar film, after which it was removed with a dissolving agent. Preparations made in this way gave very distinct pictures of the flimmer covering on the flagella. We have also tried KIRKPATRICK's method

(MACKIE & MCCARTNEY, 1942, p. 213). With this method too the flimmer covering on the flagella was seen, but the method did not give such handsome results, this complicated process being rather difficult to execute.

As regards the "plasmatic collar" there has been a diversity of opinion in the course of time, no doubt because of the extreme fineness and hyalinity of the organ. In the living condition this organ is in fact, even with the best microscope, only seen as fine lines from the cell up each side of the flagellum, for which reason already the earliest authors interpreted what they saw as a funnel-shaped plasmatic collar, just as they observed that it could be stretched out and withdrawn and expand like a funnel, and then with a jerk contract conically round the flagellum (JAMES-CLARK, 1868, KENT, 1880-82, STEIN, 1878, BÜTSCHLI, 1878). FRANÇÉ (1897) advanced the view that the collar is in reality formed like a spirally coiled membrane; this conception is used to explain the way in which the cell takes nourishment (see SENN, 1900). Later investigators (BURCK, 1909, GRIESSMANN, 1914, LAPAGE, 1925) deny this, however, and return to the original view of the "collar" as an infundibular organ. Some few authors have, however, observed that the collar may show a certain longitudinally striped structure. Thus GRIESSMANN (1914), on fixing in osmic vapour and staining with dahlia dissolved in acetic acid or with methyl violet saw the whole of the collar resolve into a varying number of fine stripes or fibres which would sometimes ramify. He does not know, however, whether this is a shrinking phenomenon or there is a precipitation. HOFENEDER (1925) saw the collar somewhat longitudinally striped, and he interpreted it as a folding; further, he regarded the collar as formed of fused pseudopods. BOYE PETERSEN (1929) by mordanting and staining according to LÖFFLER has seen the collar resolved into fine threads, but no one else seems to have observed anything similar, and these observations have not been incorporated in the current textbooks and hand-books (DOFLEIN-REICHENOW, 1949 and HALL, 1953). In all specimens which we have photographed with the electron microscope the collar appeared as resolved into a number of threads, and nothing has been seen which might indicate any spiral arrangement of them. In Figs. 1 and 2 may be counted ca. 38 threads of a thickness of ca.  $0.25\ \mu$ . The individual in Fig. 1 was fixed with osmic acid, dried on formvar film, and shadowed. The threads are seen to be quite clear, non-granular, and evidently of a soft consistency. They must therefore be regarded as fine plasmatic threads or tentacles. On the bearing of the plasmatic collar on the taking up of nourishment various papers have been written. The

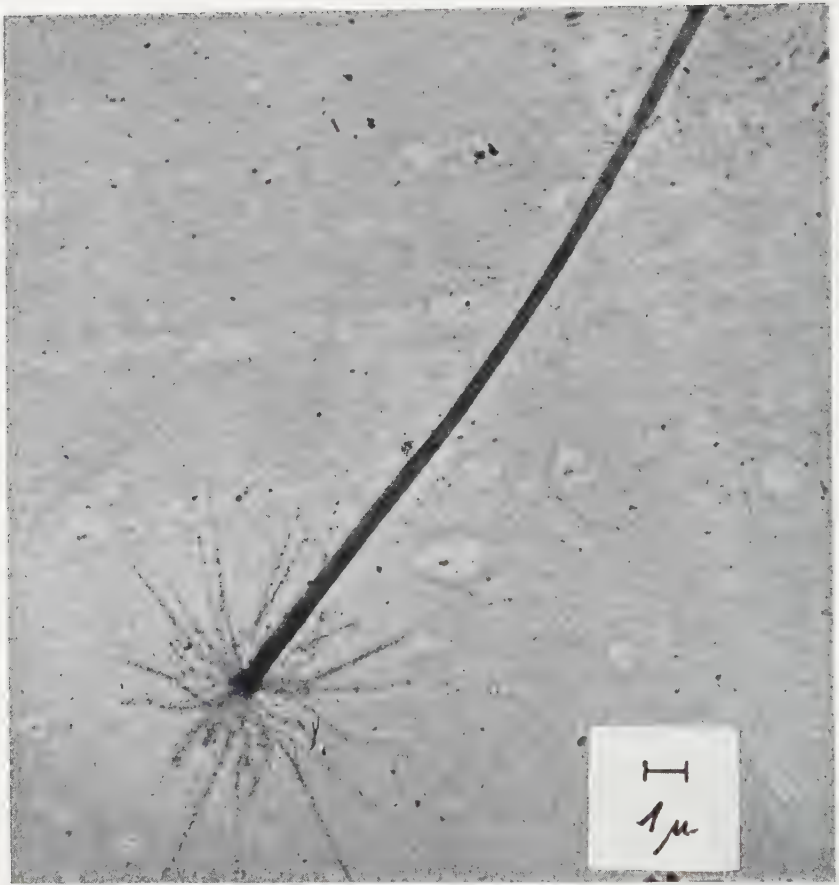


Fig. 6. Basal part of the stalk. Dried in the living state, palladium shadowing. Initial enlargement 650  $\times$ , total 5550  $\times$ .

general view is that small bodies carried forward from behind by the current set up by the vibration of the flagellum get caught in the tentacles, and this we, too, have observed. The general view is that the small bodies then move down the tentacles and are disposed in a nutritive vacuole at the edge of the envelope (LAPAGE, 1925). The flagellum is seen as a distinct whip-lash flagellum with a thin tip. It may attain a considerable length. While the cell is about 10  $\mu$  long and 9  $\mu$  broad, the thick part of the flagellum attains 25  $\mu$  or more, the thin part 5  $\mu$ . In the thick part may be seen a central more solid part, which in the picture (Fig. 7) seems to consist of fibres, apparently indicating that it has a similar structure as that described by I. MANTON and co-workers for the flagella of various organ-



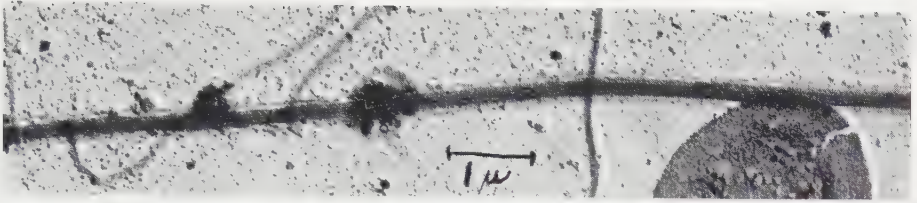


Fig. 7. Part of the flagellum showing clearly the internal fibrillar structure. Treatment as in fig. 6. Initial enlargement  $1600\times$ , total  $11,000\times$ .

isms (see MANTON and CLARKE, 1952). It is surrounded by a clearer sheath. The flagellum is ca.  $0.40\mu$  thick, the central part having a thickness of ca.  $0.25\mu$ . In slides prepared by drying and shadowing with palladium only this is seen. But after mordanting and staining the thick part of the flagellum is seen to be surrounded by a zone ca.  $2\mu$  broad on both sides. This zone begins down between the fibres of the collar and extends upwards towards the place where the whip-lash thread begins and where it is cut off straight. This zone, which has previously been described by BOYE PETERSEN (1929), is only mentioned by VLK (1938, p. 472, Abb. 8 b). After mordanting and staining according to VILH. JENSEN's method, one receives the impression under the light microscope that this zone consists of a fine garniture of hairs projecting at right angles from the flagellum. With the electron microscope one also as a rule see fine threads, but often it looks as if they form a network, and in certain cases (Figs. 2 and 3) as if they fuse at the edge of the zone. In Fig. 3 it is seen that the zone extends down below the tentacle collar, and when the latter contracts to form a cone, the opening at the tip of the cone will correspond approximately to the breadth of the zone. That the structure must be extremely delicate may be inferred from the fact that a shadowing alone is not able to make it visible. We think that the cause of this is that the difference in level is smoothed out on account of the organic substances found in the film on water where the organisms are. Thus it will be seen in Fig. 4 that the flagellum on one of the individuals is thrust in under a film formed of bacteria and here even mordanting and staining cannot bring out the structure.

Now the question is what this zone actually is, and the electron micrographs cannot, in fact, give any exact information of this. One possibility is that it is a garniture of flimmer hairs which on drying come in contact or cross each other. Another possibility is that it is an envelope round the flagellum with a fibrous or reticulate structure, or a very thin border which on drying is seen to be reticulate. From the electron micrographs



nothing can be inferred as to whether the organ is in one plane or projects on all sides from the flagellum. It is a fact that the part of the flagellum in which this zone is found, is immobile during the motion, while only its upper free part moves.

The cell is surrounded by a gelatinous envelope which is very thin. This was not seen by the earlier investigators, so they described the cell as naked. The senior author, however, has often with the light microscope been able to find specimens in the stained preparations where the cell had disappeared and only the envelope remained on the stalk. This envelope was first mentioned by BÜTSCHLI (1883-87), and later by LAPAGE (1925) and is seen in the latter's figures. In Fig. 2 it is likewise plainly visible, and further it is seen to extend a short way down the stalk as a tube.

The stalk may attain a very considerable length (as much as  $192\mu$  has been measured), and it is attached below by a disc of radiating rays (Fig. 6). In the cases we have observed it was attached to the water film, but according to the literature it may also be attached to other objects, e. g. the roots of *Lemna* or diatoms. How this stalk is formed is not cleared up at present. In stained preparations we have observed a few free-swimming individuals which at the end opposite to the flagellum were furnished with a number of thin excrescences which might perhaps be the beginning of the formation of a stalk. BÜTSCHLI and FISCH think that the stalk is hollow. This, however, has hardly been established with certainty (LAPAGE, 1925). In Fig. 6 (particularly on the original plate) it can be seen that it is tubular, possibly containing dried-up lumps of plasma. When broken, it presents the same characteristic appearance as a rubber tube with an abrupt bend.

As the principal result of this little investigation it may be established (1) that the "collar" in *Codonosiga* is a ring of very fine soft tentacles, (2) that in the thick part of the flagellum there is a zone, ca.  $2\mu$  broad on both sides, but it has not yet been cleared up whether this zone is a sheath round the flagellum or a garniture of flimmer hairs.

For his investigations on freshwater algae the senior author has received a grant from the Carlsberg Foundation for which he here offers his respectful thanks.

In the present investigations we have had the invaluable aid of Mr. FRITS CARLSEN, M.Sc., from the Biophysical Institute of the University, and we thank the Director of the Institute, Professor Dr. H. M. HANSEN, for permission to use the electron microscope.

## Bibliography.

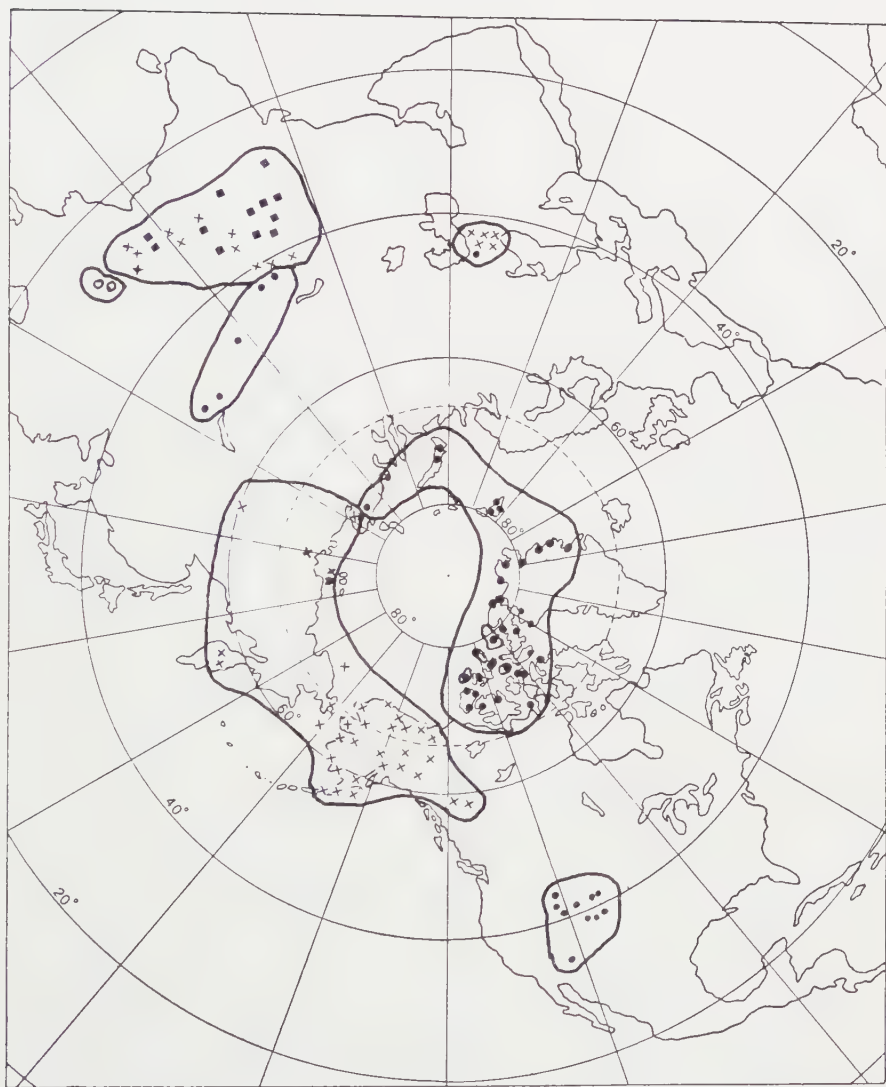
- BÜTSCHLI, O., 1878: Beiträge zur Kenntnis der Flagellaten etc. I. Zeitschr. f. wiss. Zoologie 30.
- 1883–87: Mastigophora in: Bronn's Klassen und Ordnungen des Tierreiches 1, Abt. 2.
- BURCK, C., 1909: Studien über einige Choanoflagellaten. Arch. f. Protistenkunde 16.
- DOFLEIN-REICHENOW, 1949–1953: Lehrbuch der Protozoenkunde. 6 Aufl. Jena.
- FISCH, C., 1885: Untersuchungen über einige Flagellaten etc. Zeitschr. f. wiss. Zoologie 42.
- FRANCÉ, R. H., 1897: Der Organismus der Craspedomonaden. Budapest.
- GRIESSMANN, K., 1914: Ueber marine Flagellaten. Arch. f. Protistenkunde 32.
- HALL, R. P., 1953: Protozoology. New York.
- HOFENEDER, K., 1925: Ueber eine neue Craspedomonadine. Arch. f. Protistenkunde 51.
- JAMES-CLARK, J., 1866: On the structure and habits of Anthophysa Mülleri Bary etc. Ann. Mag. Nat. Hist. 3, 18.
- 1868: On the spongiae as infusoria flagellata etc. Ibidem 4, 1.
- KENT, W. S., 1880–82: Manual of the infusoria. London.
- LAPAGE, G., 1925: Notes on the Choanoflagellate Codonosiga botrytis Ehrb. Quart. Journ. of Microscopical Science. N. S. 69.
- MACKIE, T. J. & MCCARTNEY, J. E., 1942: Handbook of practical bacteriology. 6. ed. 1942.
- MANTON, I. & CLARKE, C. B., 1952: An electron microscope study of the spermatozoid of Sphagnum. Journ. of Experimental Botany. 3.
- PETERSEN, JOHS. BOYE, 1929: Beiträge zur Kenntnis der Flagellatengeißeln. Bot. Tidskr. 40.
- SENN, G., 1900: Flagellata in: Engler & Prantl. Die natürlichen Pflanzenf. 1, 1, a.
- STEIN, F., 1878: Der Organismus der Infusionsthier. 3. 1. Hälfte. Leipzig.
- VLK, W., 1938: Ueber den Bau der Geißel. Arch. f. Protistenkunde. 90.

## The North American Races of *Saxifraga flagellaris* WILLD.

By A. E. PORSILD

The first North American collection of *Saxifraga flagellaris* of which we have knowledge came from Cape Newenham, in Kuskokwim Bay, Alaska, and was made in 1778, by DAVID NELSON, a gardener and botanical collector from Kew Botanical Gardens, who was sent out by Sir JOSEPH BANKS to assist WILLIAM ANDERSON, surgeon and naturalist to Captain COOK's 3rd expedition, in the *Resolution* and *Discovery*. The botanical collections made by DAVID NELSON were deposited in BANKS' private herbarium, and there the Cape Newenham plant remained unnamed until FREDERICK PURSH (1814) saw and described it as *Saxifraga setigera* PURSH. Five years later, ROBERT BROWN, who was then librarian to Sir JOSEPH, realized that the Cape Newenham plant was inseparable from a plant from Caucasus which WILLDENOW (1810) had described as *S. flagellaris*. ROBERT BROWN (1819) was then engaged in the naming of a small collection of plants brought back from Baffin Bay by JOHN ROSS. Among the ROSS plants BROWN found a second North American collection of *S. flagellaris*, most likely collected at Possession Bay on Bylot Island. About this time abundant and more complete material of this curious plant had been collected in Melville Island by officers of PARRY's 1st Voyage for the discovery of the North-West Passage, in the years 1819–20. Their extensive botanical collections, likewise, were turned over to ROBERT BROWN and formed the basis of his classic work on the flora of Melville Island (1824) in which he gave the first detailed description of *S. flagellaris*. Although BROWN did not realize it, his careful and accurate description of the calyx clearly shows that the plant from Melville Island differed from that of Cape Newenham as well as from WILLDENOW's plant from Caucasus.

W. J. HOOKER, who had more and better material of North American *S. flagellaris*, when preparing the first volume (1834) of his *Flora Boreali-*



World distribution of *Saxifraga flagellaris* WILLD. Solid dots: ssp. *platysepala* (*S. setigera* LOS. not PURSH; *S. Crandallii* GAND.; *S. Komarovii* LOS.). Crosses: ssp. *flagellaris* (*S. setigera* PURSH). Solid squares: ssp. *mucronulata* (*S. mucronulata* ROYLE). Rings: ssp. *megistantha*.

Americana, was the first to notice that the plants collected by PARRY and Ross differed in some important respects from those brought back from the Canadian Rocky Mountains by DRUMMOND and other members of the FRANKLIN Expeditions (1819–27). HOOKER wrote (p. 254):

“We find a remarkable difference between our Arctic Sea-shore and Island specimens, and those from the Rocky Mountains of the interior; the former having almost universally a single-flowered stem, and ovary partly inferior and broad calycine segments; while the latter have several flowers on the stem, a free ovary, and narrow sepals or at least a deeply 5-partite calyx; and appearing to correspond almost very (*sic*) particular with the European state of the plant, as far as can be judged by the figure of STERNBERG; still we have only considered the two as varieties”.

The Rocky Mountain plant he thus merely designated var. “ $\alpha$ . caule 1–5-floro, ovario omnio libero, sepalis oblongis”, while the arctic plant was set apart as var. “ $\beta$ . caule sub-1-floro, ovario basi adhaerente, laciniis calycinis ovatis”. Strangely enough he gave *S. setigera* PURSH as synonym for the latter, although an examination of the type (the Cape Newenham plant) in the British Museum (Natural History) in London clearly shows that it<sup>1</sup>), like all other *S. flagellaris* from Alaska, is inseparable from the plant of the northern Canadian Rocky Mountains and from *S. flagellaris* of WILLDENOW.

Although HOOKER so well described the difference between the two plants, and in his fine plate (l. c., tab. 87) gave excellent detailed drawings of the floral parts, he failed to realize that each occupied perfectly distinct and well-defined geographical areas, and it was left to TRAUTVETTER (1847) who recognized both varieties in collections made by MIDDENDORFF in Taimyr Peninsula, to give names to HOOKER's var.  $\alpha$ . and  $\beta$ . The first he called var. *stenosepala*, the second, var. *platysepala*. Their presence in Taimyr Peninsula where var. “*stenosepala*” reaches the east side near the mouth of Khatanga River while var. *platysepala* along the west coast extends north to Cape Chelyuskin has been confirmed by KJELLMAN (1882). Before TRAUTVETTER, TORREY and GRAY (1838–40) had accepted HOOKER's var.  $\alpha$ . and  $\beta$ . without, however, adding any new information. In view of SMALL's readiness to recognize the significance of even minor morphological differences, it is strange that, when (1905) transferring *S. flagellaris* to the genus *Leptasea*, he accepted the species in a broad sense, apparently failing to notice the remarkable difference in the shape of the calyx so clearly shown in HOOKER's plate which he cited, and presumably had seen. Accordingly, he stated the range of

<sup>1</sup>) As kindly verified by Mr. EXELL, in a letter dated February 6, 1952, from Dr. G. TAYLOR, Keeper of Botany, British Museum.



*Leptasea flagellaris* (WILLD.) SMALL as "circumboreal and alpine, extending southward in the Rocky Mountains to Arizona", as did RYDBERG (1917 and 1922) in both editions of his Rocky Mountain Flora.

Meanwhile, the extensive botanical exploration of the high mountains of central Asia which began in the latter part of the 19th Century, had added many new stations for *S. flagellaris* and also several new, more or less closely related species: *S. flagellaris* ssp. *mucronulata* (ROYLE) ENGL. & IRMSCH., *S. Brunoniana* WALL, and *S. Josephi* ENGLER, while more recently yet another distinct race, *S. flagellaris* ssp. *megistantha* HAND.-M.ZT. has been discovered in northwestern Yunnan (HANDEL-MAZETTI 1936).

ENGLER and IRMSCHER (1916) divided *S. flagellaris* into ssp. *mucronulata* (ROYLE) ENGL. & IRMSCH. and ssp. *euflagellaris* ENGL. & IRMSCH. Under the latter they recognized var. *stenosepala* and var. *platysepala*, and for each described three minor "forma". But they did not consider them geographical races, stating for var. *stenosepala*: "Verbreitung im ganzen Areal der Art mit Ausnahme der Rocky Mountains", and for var. *platysepala*: "Verbreitung im ganzen Areal der Art, selten im Kaukasus". This view is certainly erroneous, for in the light of our present information it is quite evident that, in North America at any rate, there are two well-defined geographical races, readily separated on the following characters:

Hypanthium broadly campanulate, green and, like the linear-oblong free sepals, lacking purple-headed, stalked glands; petals deep yellow; ovary free or almost so.

ssp. *flagellaris*<sup>1)</sup>

Amphi-Beringian; arctic-alpine

Hypanthium turbinate, dark purple; sepals ovate-oblong, united in their lower third and, like the hypanthium, covered with purple-headed, stalked glands; petals pale yellow; base of the ovary attached.

ssp. *platysepala*

Amphi-Atlantic; higharctic

<sup>1)</sup> *Saxifraga flagellaris* WILLD. ssp. *flagellaris*.

*S. flagellaris* WILLD. in STERNB. Revis. (1810) 25, tab. 6, as to type.

*S. setigera* PURSH Fl. Am.-Sept. (1814) 312.

*S. flagellaris* WILLD. var. *α* HOOK. Fl. Bor.-Am. (1834) 253, tab. 87 A.

*S. flagellaris* WILLD. var. *stenosepala* TRAUTV. Fl. Taimyr. in MIDDENDORFF Sib. Reise (1847) 1, 2: 42.

*Saxifraga flagellaris* WILLD. ssp. *platysepala* (TRAUTV.) n. comb.

*S. flagellaris* WILLD. var. *platysepala* TRAUTV. Fl. taimyr. in MIDDENDORFF Sib. Reise (1847) 1, 2: 42.

*S. flagellaris* WILLD. var. *β* HOOK. Fl. Bor.-Am. (1834) 253, tab. 87 B.

*S. Crandallii* GAND. Bull. Soc. Bot. Fr. (1918) 65: 30.

*S. Komarovii* LOS. in Fl. U.S.S.R. (1939) 9: 162 & 486, tab. ix, fig. 10.

*S. setigera* sensu LOS. in Fl. U.S.S.R., not PURSH.

An examination of the ample material in the GRAY Herbarium of *S. flagellaris* s. lat. from the central Asiatic highlands failed to reveal any consistent differences between W. American and E. Asiatic var. "*stenosepala*" and the narrow-sepalled plant of the central Asiatic highlands. Likewise, specimens of ssp. *platysepala* from arctic America, Greenland, Spitsbergen and Novaya Zemlya completely match broad-sepalled ones from arctic western Siberia, Altai and Tien Shan. Amply distinct from both are ssp. *mucronulata* in which the flagellae are glandular-pilose and the petals obovate-oblong, only twice as long as the sepals, their base narrowed and almost claw-like. In the GRAY Herbarium is a single collection of ssp. *megistantha* from mountains northeast of Yangtze-Mekong watershed, 14,000 feet elevation, J. F. ROCK, No. 10316, June, 1923, showing a plant which is undoubtedly closely related to ssp. *flagellaris* from which it differs by less leafy flowering stem and larger flowers with broadly obovate petals.

The situation is not entirely clear in the U.S.S.R. LOSINA LOSINSKAJA in Fl. U.S.S.R. (1939) in the Sect. *Hirculus*, Ser. *Flagellares* recognized three species:

(1) *S. flagellaris* WILLD. which is said to have broadly campanulate flowers with the calyx cleft to the base, and narrowly elliptical sepals, 2-4 mm long and 1-1.5 mm wide. This clearly is ssp. *flagellaris* and for it LOSINSKAJA gives the following distribution: Arctic: Arctic Siberia; eastern Siberia: Dahuria, Angara-Sajan; Far East: Kamchatka; Caucasus: Cisural. General Distr.: Beringia, Alaska, Mongolia.

(2) *S. setigera* PURSH is said to have funnel-shaped flowers and densely glandular peduncles, a well-developed hypanthium, calyx densely glandular, cleft to the middle, its segments blunt and its ovary half free. These characters, and the illustration (l. c., tab. 9, figs. 12, 12a and b) clearly shows that ssp. *platysepala* is meant but that LOSINSKAJA was misled by W. J. HOOKER (l. c.) who, as shown, erroneously placed *S. setigera* in synonymy under his var.  $\beta$ . The distribution given for the "false" *S. setigera* is as follows: Arctic: Novaya Zemlya, arctic Siberia, west Siberia, Altai, central Asia, Tien Shan. General Distr.: Arctic Europe, North America.

(3) *S. Komarovii* A. Los., judging from the detailed description and the rather crude figure (l. c., p. 162 and 486, tab. 9, figs. 10, 10a and b), is intermediate between ssp. *flagellaris* and ssp. *platysepala*. The main difference as stated in the key (l. c., p. 141) is that the leaf-margins of *S. Komarovii* are said to be "glandular" whereas in the other two they are said to be "ciliate". This character, especially when based on a single collection, is of small significance because in the young leaves of both ssp. *flagellaris* and ssp. *platysepala*, the setae on the leaf-margins are gland-tipped as shown, e. g. in LEDEB. Ic. Fl. Ross. tab. 321 or Fl. Dan., tab. 2353 (the latter from Spitsbergen). The distribution given for *S. Komarovii* is: Central Asia: Pamir-Alai, but the plant apparently is known only from the type collection: Seravschan, Sabak, July 27, 1893, V. L. KOMAROV (Type in Leningrad).

The two races of *S. flagellaris* afford an interesting type of geographical distribution of the type which HULTÉN (1937, map 29) has called "Eurasian arctic-montane". As shown in map (Fig. 1), ssp. *platysepala* is a high-arctic, Amphi-Atlantic race with a range extending from western Siberia over Novaya Zemlya, Spitsbergen and northern Greenland across the Canadian Archipelago, but not reaching Alaska. In common with a number of other wide-ranging arctic plants<sup>1)</sup> it has a disjunct area far south in the Rocky Mountains, on high peaks of Colorado, Utah and Arizona where it has been called *S. Crandallii* GAND.; similarly isolated and disjunct populations are found in the highlands of Pamir, Tien Shan, and Altai of central Asia (*S. Komarovii* A. LOS. and *S. setigera*, *sensu* A. LOS., not PURSH).

The main areas occupied by ssp. *flagellaris* are northwestern North America and northeastern Asia where ssp. *platysepala* does not occur. Disjunct and isolated populations are found in Kashmir, west Tibet, and Caucasus. Only in Caucasus, Pamir, and in Taimyr Peninsula of arctic western Siberia have the two races been reported occurring in the same general area, although, apparently not ever together.

The fact that, besides the subspecies *flagellaris*, *platysepala*, *mucronulata* and *megistantha*, other closely related species (*S. Brunoniana* WALL, *S. Josephi*, *S. microgyna* ENGL. & IRMSCH., and *S. pilifera* HOOK.) occur in the central Asiatic highlands suggests that this was probably the centre of origin of *S. flagellaris* and that it survived there during the maximum advances of the ice sheets that once bisected central Siberia occupying the central Siberian plateau between Yenisey and Lena Rivers, or that the original population was split by the ice and survived in several different areas in central Asia. In post-glacial time one branch (ssp. *platysepala*), possibly by way of the western edge of the plateau, dispersed northward to the arctic coast and thence over Novaya Zemlya, Spitsbergen and Greenland to the North American Arctic while the other branch (ssp. *flagellaris*) dispersed from central Asia, south of the ice cap, by way of the unglaciated Chersky, Kolyma, and Anadyr Ranges, crossing Beringia to America where it occupied Alaska, Yukon, and mountains of northern Mackenzie District and British Columbia.

In North America at least, both races of *S. flagellaris* have similar ecological requirements: both are obligate calcicoles and, in the Arctic at least, are not known to occur outside the calcareous sediments. Both

<sup>1)</sup> *Phippsia algida*, *Armeria maritima* ssp. *labradorica*, *Juncus biglumis*, *Koenigia islandica*, *Sagina caespitosa*, *Campanula uniflora*, to mention only a few.

have a pronounced preference for open, well-drained, gravelly soils that during the growing season are well supplied with water, commonly from melting snowbanks. Both are well adapted to frost-heaved soils and although occasionally growing among slow-growing mosses and lichens, neither race is able to compete successfully with more aggressive phanerogams and for this reason are never found in closed tundra communities. Both are well equipped for rapid dispersal over land surfaces sparsely covered or devoid of vegetation and therefore successful pioneers on freshly exposed moraines and fjaeldmark. Neither is able to disperse across closed tundra communities.

Both races depend mainly on vegetative reproduction for which they are particularly well equipped by their long, flagellate runners terminating in small, freely rooting rosettes, but reproduce by seed as well. For *ssp. flagellaris* this may even be the rule, except at high elevations; in *ssp. platysepala* sexual reproduction is known to take place, at least occasionally even in high latitudes (Cape Sheridan, Ellesmere Island, lat. 82° 30' N., J. KELSALL, No. 52 CAN), and in Banks Island, in 1949, it was one of the few phanerogams that succeeded in maturing seeds following an exceptionally cold summer (PORSILD, No. 17775). According to WARMING (1909) the flowers of *S. flagellaris* are protogynous although subsequent self-pollination appears to be the rule. In Banks Island the daughter plants were noted occasionally to flower when still attached to the mother plant. A single flower is perhaps the rule for *ssp. platysepala* though 2- or even 3-flowered specimens are by no means rare and have been collected in Prince Patrick Island and in northernmost Ellesmere Island.

Although it reaches the north slope of Brooks Range in Alaska, Wrangel Island, and Taimyr Peninsula, *ssp. flagellaris* apparently is less arctic in habit than *ssp. platysepala*. Generally it is a taller and more vigorous plant with flowering stems 10-15 cm tall, bearing from 1-7 flowers; its stolons may occasionally reach a length of 30 cm. Like *ssp. platysepala* it is decidedly alpine and in the Bering Sea region of Alaska is one of the species which the writer (PORSILD, 1939) noted as being restricted to levels above the 1000 foot mark.

### References.

- BROWN, R., 1819: App. to John Ross' Voyage of Discovery etc., 2. London.  
 — 1824: in Suppl. to the App. of Capt. Parry's Voy. for the Discovery of a North-West Passage in the years 1819-20. London.  
 ENGEL & IRMSCHER, 1916: Pflanzenreich, IV, 117, 1. Leipzig.

- HANDEL-MAZZETTI, H., 1929-1936: *Symb. Sin.* pt. 7. Wien.
- HOOKE, W. J., 1834: *Flora Boreali-Americana*. London.
- HULTÉN, E., 1937: Outline of the history of arctic and boreal biota during the Quaternary Period. Stockholm.
- KJELLMANN, F. R., 1882: *Sibiriska Nordkustens Fanerogamflora*, Vetensk. Iakttagelser, 1. Stockholm.
- LOSINSKAJA, L., 1939: in *Fl. U.S.S.R.*, 9. Moskva.
- PORSILD, A. E., 1939: Contributions to the Flora of Alaska, *Rhodora* 41: 141-301.
- PURSH, FREDERICK, 1814: *Flora Am.* - Sept., London.
- RYDBERG, P. A., 1917 and 1922: *Fl. Rocky Mountains and adjacent Plains*, New York.
- SMALL, J. K., 1905: *N. Am. Flora*, 22, p. 154. New York.
- TORREY, JOHN, & GRAY, ASA, 1838-40: *Fl. of North America*. New York.
- TRAUTVETTER, E. R. v., 1847: *Florula taimyrensis phaenogama*. In MIDDENDORFF, *Sibirische Reise*, 1, 2. St. Petersbourg.
- WARMING, EUG., 1909: Structure and biology of arctic flowering plants, *Medd. o. Grl.* 36. København.



## Experimental and Cytological Studies in *Plantago media*

By KNUD RAHN

The author has had the pleasure to participate in the experimentally taxonomic and cytological investigations into a number of plant species made in Copenhagen under the leadership of Professor T. W. BÖCHER. *Plantago media*, which is the subject of the present paper, is one of the species included in these investigations.

The majority of the seed samples have been collected by Professor T. W. BÖCHER and Cand. mag. K. LARSEN, a single sample by Professor E. LEHMANN, Tübingen, and one (no. 2438) has been sent from the Botanical Garden of Zagreb.

The strains were all raised from seed and cultivated at Vridsløselille on an experimental field belonging to the Botanical Garden of the University of Copenhagen. The measurements were made at Vridsløselille, while the cytological work was carried out at the Botanical Laboratory of the University.

The chromosome number was examined in 24 samples from Western Europe (see Fig. 1); 18 of them showed  $2n = 24$ , which is in accordance with previous countings by McCULLAGH (1934), SUGIURA (1939), and TURESSON (1938) (material from Budapest and Omsk), while 6 samples showed  $2n = 12$ . Four of these originated from the neighbourhood of Bilbao in Northern Spain, one from Gavarnie in the Pyrenees, and one from St. Jean de Luz in the southwesternmost part of France.

As shown by McCULLAGH (*l. c.*) the basic number in the genus *Plantago* is 6; the former group must, therefore, be considered as tetraploids, the latter as diploids. Among the tetraploids it was often difficult to ascertain the occurrence of more than two chromosomes with satellites, but in one case (Fig. 2b) four satellites were clearly seen. In the diploid strains two chromosomes with satellites were found (Fig. 2a).

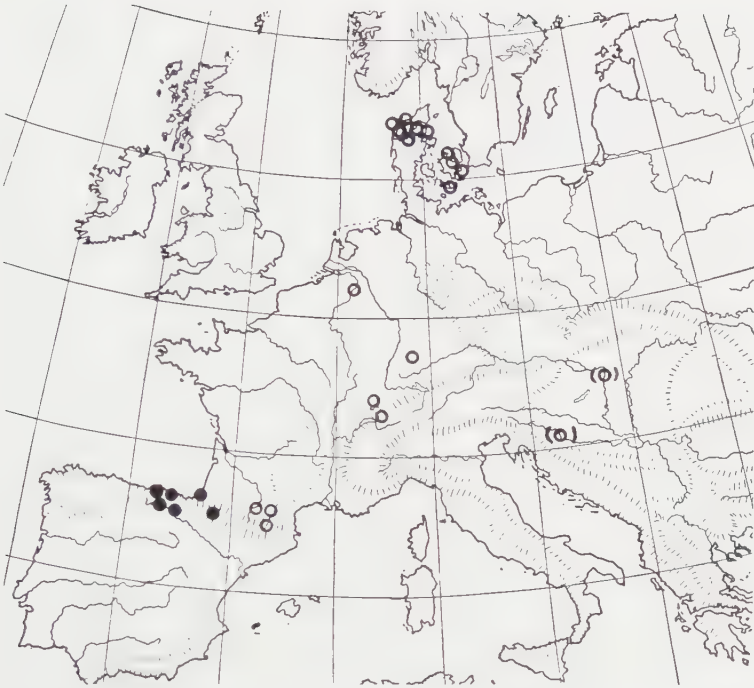


Fig. 1. Distribution of diploid and tetraploid *Plantago media*. The dots are diploids, the open circles tetraploids. Two of the circles are in parenthesis; one of the strains thus denoted, originating from wild sources in Yugoslavia, has been sent from the Botanical Garden of Zagreb, but without exact statement of origin; the other dot indicates TURESSON's counting from Budapest (1938).

MCCULLAGH found that the various chromosome types were present in a multiple of 4, with the exception that only two of the four chromosomes with terminal centromeres had satellites. This fact led MCCULLAGH to suggest that *Plantago media* originated as a hybrid.

Meiosis was examined in two tetraploid strains (Nos. 1892 and 2251) and as a rule seemed to take quite a normal course with the formation of twelve bivalents. Still, the possibility of development of multivalents in a few cases could not be excluded. In both strains it could clearly be ascertained that in several PMC's there was a single univalent chromosome; in anaphase I this was seen as a laggard (Fig. 2c) and sometimes it might be seen to have divided in telophase I.

In no. 1892 it was now and then possible to observe a bridge and an acentric fragment in anaphase I (Figs. 2d and e), and a bridge in anaphase

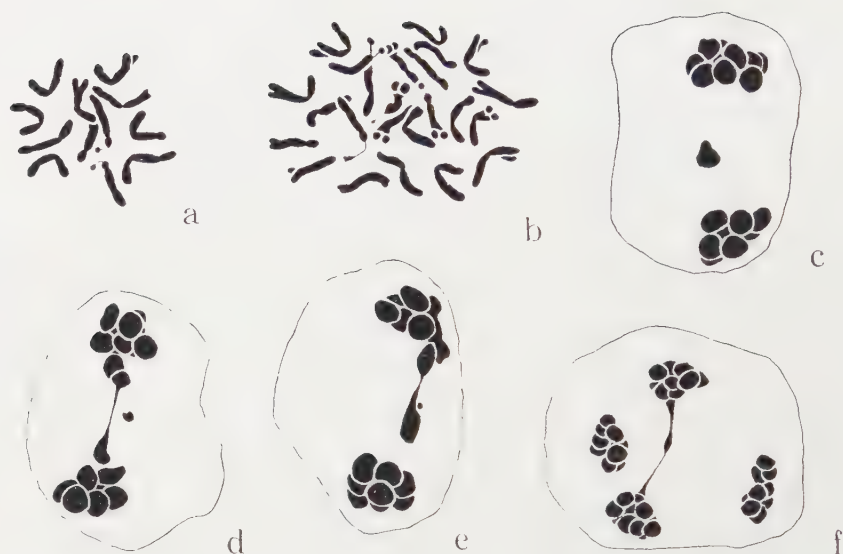


Fig.2. a-b: Mitoses from root-tips of *Plantago media* (Fixation: Navashin-Karpechenko. Staining: Newton's gentian violet). a: no. 1398,  $2n = 12$ . b: no. 2251,  $2n = 24$ . c-f: Meiosis in PMC of tetraploid *Plantago media* (no. 1892) (Fixation: Carnoy and Navashin-Karpechenko. Staining: Feulgen). c: late anaphase I with a lagging univalent. d-e: late anaphase I with an inversion bridge and an acentric fragment. f: late anaphase II with a bridge.

II (Fig. 2f). This shows that the strain in question is a structural hybrid as regards an inverted segment.

The result of the measurements appears from Table 1. Most of the plants were measured in the third year after sowing; the remaining ones in the second year. Still, it should be possible to compare all the measures, as *Plantago media* seems to grow but insignificantly after the second year.

TURESSON (1932) cultivated two strains of *Plantago media*, one from the lowlands in Southern Sweden and one from the alpine region in Jämtland. The former had an average height of 65 cm, the latter a height of 40 cm, and the alpine strain flowered about one week before the lowland plants. TURESSON concluded (l. c.): "Es soll jedoch hervorgehoben werden, dass das ausserskandinavische Material von Mittel- und Südeuropa aus noch späteren und noch etwas höheren Biotypen zusammengesetzt sich erwiesen hat als das südschwedische." In the present material it has not been possible to point out any correlation between origin and time of flowering; still, the diploids may be flowering a little later than most tetraploids. The southern tetraploids prove not to be taller than



Fig. 3. The diploid no. 1322 on the experimental field at Vridsløselille. Note the length of the spikes in relation to the scapes. – (Phot. T. W. BÖCHER).

many northern plants; a very small type (No. 2307) has even come from Tübingen in South Germany.

The smallest of the tetraploids (No. 2910) originates from Bulbjerg, a greatly wind-exposed cliff on the northwestern coast of Jutland; besides being of low growth the plants are characterized by having rather thick spikes. Nos. 3002, 3003, and 3004 have also been collected in Northwest Jutland, the first two at a distance from the coast and the third on a cliff on the Limfjord; they have a low growth, similar to that of no. 2910, but normal spikes. The windy climate by the North Sea tries to eliminate the tall biotypes, in the same way as near the Swedish west coast, as pointed out by TURESSON (1925 and 1930). From Bulbjerg Professor BÖCHER has several other plants in culture. They are all characteristic

Table 1.

Cult No.	Origin	2n	Year of sowing	Year of measurement	Number of plants
1370	Peña Bargindia, Spain . . . .	12	1950	1952	9
1363	Bilbao, Spain . . . . .	12	1950	1952	12
1522	Gavarnie, S. France . . . . .	12	1950	1952	3
1398	Vitoria, Spain . . . . .	12	1950	1952	6
1322	St. Jean de Luz, S. France . .	12	1950	1952	9
1411	Sierra Cantabrica, Spain . .	12	1950	1952	5
2910	Bulbjerg, Denmark . . . . .	24	1952	1953	15
2307	Tübingen, Germany . . . . .	24	1950	1952	12
3004	Hanklit, Denmark . . . . .	24	1952	1953	19
3002	S. of Thisted, Denmark . . .	24	1952	1953	11
3003	N. of Thisted, Denmark . . .	24	1952	1953	18
2676	Løgstør, Denmark . . . . .	24	1951	1953	17
2911	Knuthenborg, Denmark . . .	24	1952	1953	13
2251	Boserup, Denmark . . . . .	24	1950	1952	14
1750	Savoie, France . . . . .	..	1950	1952	12
3005	Klintebjerg, Denmark . . . .	24	1952	1953	19
1892	Le Sépay, Switzerland . . . .	24	1950	1952	10
2052	Pieterberg, Holland . . . . .	24	1950	1952	9
1661	Formigueres, S. France . . .	24	1950	1952	10
2017	Court, Switzerland . . . . .	24	1950	1952	18
1654	Quillan, S. France . . . . .	24	1950	1952	14
1657	Foix, S. France . . . . .	24	1950	1952	3
2438	Zagreb, Yugoslavia . . . . .	24	1950	1952	9
2667	Kongerslev, Denmark . . . .	24	1951	1953	18
2858	Stevns Klint, Denmark . . . .	24	....	....	..

by being low (e. g. *Dactylis glomerata*, *Holcus lanatus*, and *Hypochoeris maculata*).

The difference between diploids and tetraploids first of all manifests itself in the size. The length of spike + scape is in all diploids on an average  $28.71 \pm 0.86$  cm ( $\sigma = 5.68$ ), while in all tetraploids it is on an average  $41.17 \pm 0.70$  cm ( $\sigma = 10.80$ ), which gives a difference between the means of  $12.46 \pm 1.10$  cm. The length of the leaves for the diploids is on an average  $11.89 \pm 0.44$  cm ( $\sigma = 2.91$ ), for the tetraploids  $18.11 \pm 0.38$  cm ( $\sigma = 5.74$ ). The difference between the means is  $6.22 \pm 0.58$  cm. The length of the spikes is almost the same in diploids and tetraploids (dipl.:  $M = 11.18 \pm 0.37$  cm,  $\sigma = 2.43$ ; tetrapl.:  $M = 10.23 \pm 0.20$  cm,  $\sigma =$



Table 1 (continued).

Length of longest spike + scape in cm		Length of longest spike in cm		Length of longest leaf in cm		Length of (spike + scape) : spike length	
Average	(Range)	Average	(Range)	Average	(Range)	Average	(Range)
22.4	(8-31)	9.6	(4-15)	8.7	(4-12)	2.4	(1.7-3.2)
27.6	(22-38)	11.4	(9-14)	12.5	(9-17)	2.4	(1.9-2.9)
	(25-32)		(10-13)		(8-15)		(2.5-2.9)
31.2	(28-35)	10.0	(9-12)	11.8	(9-18)	3.2	(2.5-3.9)
32.0	(28-39)	12.8	(11-15)	14.2	(13-15)	2.5	(2.2-2.8)
33.2	(32-35)	12.0	(10-16)	12.2	(11-13)	2.8	(2.2-3.3)
25.7	(20-32)	7.8	(6-9)	15.7	(13-20)	3.4	(2.2-4.7)
31.1	(21-52)	8.2	(6-12)	10.0	(6-16)	3.8	(3.1-4.4)
31.2	(26-37)	8.4	(5-12)	11.6	(8-19)	3.9	(2.6-5.2)
32.2	(20-39)	7.6	(6-12)	14.4	(9-20)	3.9	(3.3-4.9)
33.0	(16-45)	8.6	(3.5-12)	17.3	(8-25)	4.1	(3.1-6.4)
39.3	(26-61)	8.2	(6.5-12)	20.1	(8-30)	4.9	(3.0-6.7)
40.0	(33-52)	9.0	(6-12)	18.4	(14-24)	4.5	(3.3-7.0)
41.1	(34-49)	11.3	(8-15)	21.5	(16-25)	3.7	(2.5-4.3)
41.3	(31-57)	9.8	(7-14)	14.7	(8-25)	4.3	(2.4-5.7)
41.8	(33-57)	10.7	(7-14.5)	16.9	(12-33)	4.0	(3.3-5.1)
42.9	(32-52)	9.6	(6-17)	16.4	(9-24)	4.8	(3.0-6.8)
46.5	(39-53)	11.1	(10-12)	19.8	(14-23)	4.2	(3.5-5.3)
47.7	(39-61)	12.0	(9-17)	19.5	(17-23)	4.1	(3.0-4.9)
49.2	(41-65)	12.0	(8-15)	20.4	(17-25)	4.1	(3.2-5.2)
50.2	(42-64)	15.5	(9-22)	19.6	(15-25)	3.3	(2.4-4.8)
	(39-57)		(6-16)		(14-20)		(3.6-6.5)
52.0	(44-59)	11.0	(6-17)	23.3	(17-29)	4.6	(2.9-5.7)
57.3	(40-74)	12.6	(6.5-19)	27.8	(22-38)	4.8	(3.4-6.8)
.....	.....	.....	.....	.....	.....	..	.....

3.16. Difference:  $0.96 \pm 0.42$  cm). The ratio between spike + scape and the length of spike will therefore be one of the most important differences between diploids and tetraploids. For the diploids the ratio is on an average  $2.600 \pm 0.065$  ( $\sigma = 0.432$ ) for the tetraploids  $4.113 \pm 0.058$  ( $\sigma = 0.895$ ). The difference between the means is  $1.513 \pm 0.087$ . The difference is thus more than 17 times the mean error.

The size of pollen was examined in two tetraploid and one diploid strain, the result (measured in micrometer units) being: no. 2910:  $M = 14.817 \pm 0.087$ ; no. 3005:  $M = 14.632 \pm 0.104$ , and no. 1398:  $M = 14.492 \pm 0.090$ . The difference is thus not significant. An examination of the stomata gave a similar result.



Fig. 4. No. 1750 from the West Alps is the only strain the chromosome number of which is unknown; still, it may be considered a typical tetraploid.  
(Phot. T. W. BÖCHER).

There is another difference, the number of seeds in the capsule as a rule being two in the diploids, but in the tetraploids mostly more than two.

*Plantago media*, according to PILGER (1937), is distributed over the greater part of Europe, Northern and Central Asia, Asia Minor, and Northern Iran. It would be of great interest to establish the more accurate distribution of the diploids and the tetraploids. In the years to come I hope to get further material which may throw light on it; especially material from the Mediterranean area will be of great interest.

Future investigations must also decide the systematic position of the diploids and the way in which the tetraploids may have arisen. Thus experiments have been started for the purpose of doubling the chromo-

some number of the diploid *Plantago media*, and it has been attempted to cross the diploid *Plantago media* with a *P. lanceolata* with the same chromosome number.

### Literature

- MCCULLAGH, D., 1934: Chromosome and chromosome morphology in Plantaginaceae I. *Genetica* 16: 1-44.
- PILGER, R., 1937: Plantaginaceae. *Das Pflanzenreich* IV: 269. Leipzig.
- SUGIURA, T., 1939: Studies on the chromosome numbers in higher plants. IV. *Cytologia* 10: 324-33.
- TURESSON, G., 1925: The plant species in relation to habitat and climate. *Hereditas* 6: 147-236.
- 1930: The selective effect of climate upon the plant species. *Hereditas* 14: 99-152.
- 1932: Die Pflanzenart als Klimaindikator. *Kungl. fysiografiska sällskapets i Lund förhandl.* 2, 4.
- 1938: Chromosome stability in linnæan species. *Landbrukshögskolans annaler.* 5: 405-14.

# Die Geschichte der Kulturpflanzen im Wandel der biologischen Methoden<sup>1)</sup>

VON ELISABETH SCHIEMANN

Wenn wir von den Bemühungen im Altertum, etwas vom Wesen und der Herkunft der Kulturpflanzen zu verstehen, absehen und den Blick auf die in Reformationszeitalter und Renaissance beginnende Naturwissenschaft richten, welche die induktive Methode geschaffen hat, so ist die Frage nach der Geschichte der Kulturpflanzen als wissenschaftliches Problem zuerst von ALPHONSE DE CANDOLLE aufgeworfen worden. Seitdem ist daraus ein Forschungsgebiet geworden, das in seinem Namen bereits seine Zugehörigkeit zu den beiden Hauptzweigen des wissenschaftlichen Forschens der Neuzeit zum Ausdruck bringt, — mit dem Nachdruck auf die Pflanzen naturwissenschaftliche, speziell biologische Probleme betreffend, mit dem Nachdruck auf den Wortbegriff der Kultur die geistesgeschichtliche Bedeutung der Problemstellung charakterisierend. Dieser Zwitterstellung entsprechend, die zugleich eine Vermittlerstellung ist, ist der Geschichte der Kulturpflanzen eine sehr vielseitige Methodik dienstbar gewesen, deren Resultate in Abhängigkeit von dem Wandel der biologischen und ethnologischen Kenntnisse der vergangenen hundert Jahre wir uns vergegenwärtigen wollen.

Der zur Verfügung stehende Raum erlaubt es nur in Stichworten die einzelnen Etappen und ihre jeweiligen Resultate zu skizzieren.

Es wird sich dabei zeigen, dass wir es mit einer sehr kontinuierlichen Entwicklung zu tun haben. Nicht so, dass die eine Methode die andere ablöst, um sie in Vergessenheit sinken zu lassen, sondern vielmehr auf ihr derart aufbaut, dass ihre Grundlagen erhalten bleiben, auch bis heute in gewissem Masse unaufgebar, so dass wir heute mit einer ganzen Fülle von Methoden an die gleiche Frage herantreten und unseren Antworten eine zunehmende Vertiefung und darum Sicherheit geben können.

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<sup>1)</sup> Nach einem Vortrag auf dem VIII. Internationalen Botaniker-Kongress in Paris 7. VII. 1954.

Ich möchte in der nun hundertjährigen Entwicklung einer Geschichte der Kulturpflanzen sechs Perioden unterscheiden, die jeweils durch spezielle wichtige Veröffentlichungen eingeleitet werden.

### Die I. Periode 1855–1870, die systematisch-pflanzengeographische Periode

wird eingeleitet durch die drei Namen: DE CANDOLLE, DARWIN, HEER. Ausgehend von einer auf vergleichender Morphologie beruhenden Systematik geht DE CANDOLLE der geographischen Verbreitung der Pflanzenwelt über die Erde nach und sucht ihre Ursachen in der Verknüpfung dieser beiden Betrachtungsweisen festzustellen. Dabei fand er in den Kulturpflanzen, deren Geschichte sich auf den verhältnismässig kurzen Zeitraum von wenigen Jahrtausenden unter annähernd bekannten geologischen und klimatischen Verhältnissen zusammendrängt, ein Modell für die Entwicklung der gesamten Pflanzenwelt, deren morphologische Umwandlung und räumliche Wanderung sich unter soviel komplizierteren, z. T. unbekannten Verhältnissen abgespielt hat. Mit dieser Conception zeigt sich DE CANDOLLE als einen der grossen Vertreter des Entwicklungsgedankens im 19. Jahrhundert und es kann nicht wundernehmen, wenn wir an anderen Stellen des Buches auf Gedanken stossen, die uns in ausgeprägter Weise bei dem zweiten für uns richtunggebenden Forscher, DARWIN, begegnen.

Auch DARWIN mussten bei seiner Reise um die Welt an Bord des Beagle in den Jahren 1831/36 pflanzengeographische Probleme in Fülle entgegen treten. Aber was ihn am stärksten beeindruckte, war die ausserordentliche Mannigfaltigkeit trotz in die Augen springender Verwandtschaft und die zweckmässige Anpassung an die jeweilige Umwelt.<sup>1)</sup>

Das ungeheure Material an Beobachtungen, das er mitbrachte, sichtlich, stellte sich ihm das Problem der Entwicklung der organischen Welt, das er bald auch methodisch experimentell angriff, damit wegweisend in eine spätere Zeit. Auch ihm boten sich dabei neben den Haustieren die Kulturpflanzen als ein extremes Beispiel von Mannigfaltigkeit, deren Ursachen vom Eingriff des Menschen her der Erkenntnis zugänglich sein mussten. So entstand nach langjähriger Forschung 1868 „Das Variieren der Tiere und Pflanzen im Zustande der Domestikation.“

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<sup>1)</sup> “In the year 1837 or 1838 I had become convinced that species were mutable productions.” (Autobiography).



Blieb DE CANDOLLE auch bei der spezielleren Behandlung der Kulturpflanzen ganz auf dem Boden der pflanzengeographischen Forschung, jedoch hineingestellt in einen weiteren Rahmen historischer und ethnographischer Probleme, so war Darwins Blick stärker auf die Wirkung des menschlichen Eingriffs in die Natur gerichtet, wie er sich besonders in der Selektion und Erhöhung der Variabilität äussert.

Die dritte grosse Anregung ging von OSWALD HEERS „Pflanzen der Pfahlbauten“ (1865) aus, welche die Aufmerksamkeit auf eine neue Quelle, die vorgeschichtlichen Funde richtete. Die Archäologie ist damit in die Kulturpflanzenforschung eingeschaltet. Neben die seit den Napoleonischen Feldzügen im Vordergrund stehende und als älteste angesehene antike Kultur Ägyptens treten ganz neu Anfänge des Ackerbaues in Mitteleuropa, die weit hinter die Römerfeldzüge zurückweisen, ja vielleicht so alt sein mochten, wie die des Orients.

Diese Männer mit ihren Arbeiten sind richtungsweisend für die Kulturpflanzenforschung geworden, indem sie als Quellen derselben Biologie, Ethnologie und Vorgeschichte aufdeckten; Biologie einerseits als morphologisch unterbaute Systematik und Pflanzengeographie, andererseits als experimentelle Evolutionslehre.

## In der II. Periode 1870–1900

noch ganz auf der vorigen fussend, geht die Forschung in zwei Richtungen: Von vorgeschichtlichen Zufallsfunden ausgehend wird die Geschichte der Kulturpflanzen

- a) auf historischer Grundlage zurückverfolgt bis zu ihrem ältesten Vorkommen,
- b) von dem ältesten Vorkommen ausgehend wird der botanische Zusammenhang mit der wilden Flora dieses Areals gesucht.

Diese Periode ist gekennzeichnet durch zahlreiche Einzeluntersuchungen, die auf antik klassischer Grundlage ausgelegt werden. An diesen Arbeiten sind die drei Forscher selbst mit Spezialarbeiten beteiligt; vor allem ist DE CANDOLLE's zusammenfassende Darstellung: „Origine des Plantes Cultivées“ 1883 zu nennen, die bis weit ins 20. Jahrhundert hinein an erster Stelle gestanden hat.

### III. Periode 1900–1918.

1900 wird die III., die Mendelistische Periode eingeleitet, schlagartig, durch die drei grossen genetischen Werke:

1900: Die Wiederentdeckung der Mendelschen Gesetze.

1900/01: DE VRIES' Mutationstheorie.

1903: JOHANSEN'S Lehre von der Erbllichkeit in Populationen und reinen Linien.

Bis zur IV. Conférence de Génétique in Paris 1911 ist diese Zeit, auch in bezug auf das, was für die Geschichte der Kulturpflanzen wichtig wird, rein genetisch ausgerichtet und methodisch ganz auf das Experiment, die induktive Methode eingestellt. Dabei wird für die Frage nach Entstehung und Entwicklung der Kulturpflanzen die in der zweiten Hälfte des 19. Jahrhunderts aufblühende Züchtungsarbeit an Getreide fruchtbar.

Die wesentlichen Fragen dieser bis 1918 anzusetzenden Periode sind: Entstehung der Variabilität und Entstehung der Anpassung.

### Die IV. Periode, beginnend 1918

kann man die Cytogenetische Periode nennen. Die Feststellung der Polyploidie des Weizens durch SAX und SAKAMURA 1918 löst eine intensive Verknüpfung der Analyse der Mendelistischen Genanlage mit cytologischen Untersuchungen aus: Die Feststellung der Chromosomenzahlen, Polyploidie in ihren verschiedenen Formen, Fertilität und Sterilität infolge von Kreuzung, ausgedehnt auf Art- und Gattungskreuzungen und endlich die Entdeckung der Amphidiploidie in der *Primula Kewensis* 1929 führt auf den Zusammenhang zwischen Polyploidie und Variabilität der Kulturpflanzen. Als grundlegende experimentelle Methode zur Analyse der phylogenetischen Zusammenhänge bis heute bleibt die Cytogenetik.

### V. Periode 1926–(1940).

Eine zweite pflanzengeographisch ausgerichtete Periode setzt ein mit VAVILOV'S Genzentrentheorie, vorgetragen auf dem 7. Internationalen Genetiker-Kongress in Berlin 1927. Sie bringt die weitgehend verloren gegangene Verknüpfung von Genetik mit Morphologie und Systematik und trägt das Interesse an den Kulturpflanzen und ihrer Geschichte

in die Botanik der ganzen Welt — was sich besonders auch für Amerika auswirkt. Man kann VAVILOV's „Ursprung der Kulturpflanzen 1926“ in seiner Bedeutung neben ALPHONSE DE CANDOLLE's Werk von 1870 stellen.

## VI. Periode seit 1937.

Lassen schon die beiden letzten Perioden keine Begrenzung in jüngere Zeit hinein zu, so kann man im folgenden nur vom Einsatz neuer Methoden durch spezielle wissenschaftliche Entdeckungen sprechen. Methoden, die ebenso wie die vorigen aus der Kulturpflanzenforschung nicht mehr zu streichen sind.

Eine Anfang der dreissiger Jahre einsetzende Periode der Mutationsauslösung mit dem Ziel der Erhöhung der Variabilität führt 1937 zur Entdeckung der Colchizinmethode zur Erhöhung der Polyploidiestufe durch BLAKESLEE und AVERY. Diese Entdeckung ist hervorgegangen aus der Erforschung der mutationsauslösenden Wirkung chemischer Stoffe, die neben der von STADLER 1931 schon auf Kulturpflanzen, speziell Gerste angewandten Bestrahlung zur Auslösung von Mutationen verwendet wurden (zuerst 1910 bereits von BAUR und seinen Schülern). Die Bedeutung der Colchizinmethode liegt in der Sicherheit und Eindeutigkeit des Effektes — Verdopplung des Chromosomensatzes als Folge der Einwirkung auf den Spindelmechanismus — im Gegensatz zu den zufallsmässigen Ergebnissen der anderen Agentien. Damit ist die sichere Herstellung von Autopolyploiden, sowie von Amphidiploiden aus sterilen Bastarden, deren Wichtigkeit für die Entstehung der Kulturpflanzen bereits in der IV. Periode bekannt wurde, gewährleistet. Sie wird in Verbindung mit der cytogenetischen Analyse (III. Periode) angewandt.

## Archäologisch-ethnologisches Gebiet.

Es bleibt uns noch die Aufgabe, den kurz skizzierten Rahmen durch die im einzelnen für unser Problem erzielten Ergebnisse auszufüllen. Dabei wird sich zeigen, dass, wie schon voraus erwähnt, keine der einmal erarbeiteten Methoden ganz fallen gelassen wurde, sondern, vielfach ergänzt und erweitert, der Erforschung von Entstehung und Entwicklung, d. h. der Geschichte der Kulturpflanzen dienstbar gemacht ist. Zuzur ist aber die Entwicklung auf dem archäologisch-ethnologischen Gebiet zu verfolgen. Hier haben sich seit der von der ersten Pfahlbau — Veröffentlichung von HEER 1865 ausgehenden Anregung 3 grosse metho-

dische Fragenkomplexe herausgebildet, welche die Bergung, Bestimmung und Datierung der Funde betreffen.

In der Methodik der ersten beiden lassen sich keine einschneidenden Etappen erkennen: sie wird vielmehr allmählich, aber laufend verfeinert.

### 1. Bergung.

Wurden bei den ersten Pfahlbauuntersuchungen die an die Oberfläche getretenen leichten organischen Reste mittels Sieben aufgefischt (nach der Schilderung von MESSIKOMER), so bediente man sich bald zum Hervorholen aus bestimmbarer Tiefe des Erdbohrers; dieser ist bis zu der heute üblichen Ausführung technisch verbessert worden und hat die Feststellung einer genauen Schichtenfolge ermöglicht, die bei den früheren Fundbergungen häufig so gestört wurde, dass eine spätere Auswertung nicht mehr möglich war. Das orientalische, ägyptische Material in der Zeit vor 1900 kam — zumeist als Grabfunde — als Ganzes zum Vorschein und forderte nur Vorsicht und Sorgfalt beim Präparieren nach dem Übergang aus dem trockenen Klima Ägyptens, in dem es sich so vorzüglich halten können, in die Museen Europas — eine Präparation, die in unübertroffener Meisterschaft Georg Schweinfurth geübt hat.

Als seit 1900 zunehmend die Ausgrabungen auch im Orient direkt in den Boden gingen, machte man sich mehr und mehr die paläontologischen Methoden zu eigen, wobei die Geiseltalfunde vorbildlich waren.

Seit Mitte der dreissiger Jahre ist als neue geübte archäologische Methode die Berücksichtigung von Abdrücken von Kulturpflanzenresten (Samen von Getreide, Leguminosen und Unkräutern) in Keramikscherben wichtig geworden. Nachdem UNGER bereits in den sechziger Jahren die Einschlüsse in altägyptischen Ziegeln berücksichtigt hatte, ist diese Quelle von Funden erst um die Jahrhundertwende von SARAUEW in Copenhagen wieder aufgenommen worden und ein umfangreiches Material von Dänemark und Norddeutschland dabei zutage gefördert worden. Leider hat SARAUEW seine Ergebnisse nicht geschlossen veröffentlicht, sie sind nur von HOOPS (1905, Waldbäume und Kulturpflanzen im germanischen Altertum) z. T. verwertet worden. Im Jahre 1934 konnte ich dies Manuskript in Copenhagen einsehen und es ist im Anschluss eine internationale Zusammenarbeit, zunächst für den nordeuropäischen Raum, die nordischen Kulturen betreffend, vereinbart worden, die in den folgenden Jahren von JESSEN und seinem Mitarbeiter HELBÆK für England durchgeführt ist und z. Z. in Skandinavien und nach einer Unterbrechung seit dem Kriege in Norddeutschland von mir und Dr. HOPF fortgesetzt wird.

Es ist keine Frage, dass hier noch ein reiches unausgewertetes Material in den Magazinen der Museen liegt, das der Bearbeitung bedarf; methodisch wird es erfasst durch Abdrücke mittels Plastillin, welche ein Positiv des im Ton eingeschlossenen und beim Bruch herausgefallenen Objektes liefern.

Nur langsam zunehmend wurde die Aufmerksamkeit der Archäologen und Prähistoriker auf die Bedeutung der Kulturpflanzenfunde für die Kulturgeschichte und Ethnologie gerichtet, vor allem hat es lange an der Bestimmung der exakten Lage und an der quantitativen Erfassung der Pflanzenfunde gefehlt; man begnügte sich ihr Vorkommen überhaupt festzustellen; das Interesse lag bei der Typologie.

Heute darf man wohl sagen, dass das Verständnis vorhanden ist und kein Kulturpflanzenrest der Bergung in angemessener Weise und nach genau festgehaltener Lage entgeht oder zu entgehen braucht.

## 2. Es folgt als zweites methodisches Problem die Bestimmung der Kulturpflanzenreste.

Grundlegend bleibt die seit Beginn verwendete Methode der vergleichenden Morphologie; sie erfordert eine grosse Formenkenntnis, der zunehmend Vergleichssammlungen recenten Materiales zu Hilfe kommen. Die grösste Bedeutung kommt ihr bei der Bestimmung von Kornabdrücken in Scherben zu, die uns nur ein Negativ der ursprünglichen Form ohne substantielles Material übermitteln. Die älteren Bestimmer haben wesentlich auf morphologischer Grundlage gearbeitet (UNGER, A. BRAUN, SCHWEINFURTH, HARMS, A. SCHULZ, NEUWEILER, WERTH, JESSEN, SCHIEMANN, BERTSCH, PERCIVAL). Hinzu tritt aber bereits seit Beginn des Jahrhunderts die Verwertung anatomischer Merkmale nach den Methoden der landwirtschaftlichen Samenuntersuchung (WITTMACK), der Pharmazie (NETOLITZKY) und der Paläontologie (E. HOFMANN).

Sie findet ihre Verwendung vor allem beim Aufschluss verkohlten Materiales, besonders bei spärlichen, verletzten oder durch Brand formdefekten Fundstücken. —

In den dreissiger Jahren wird eine Diskussion über den verkohlten bzw. inkohlten Zustand der Funde wichtig, weil er über das letzte Schicksal der Fundstätte, d. h. zur Urgeschichte etwas auszusagen hat; auch hier erwiesen sich Erfahrungen der Paläontologie wertvoll.

Es ist einleuchtend, dass somit die Archäologie auf die Mitarbeit des Fachbotanikers angewiesen ist, und umgekehrt aus den so gewonnenen



botanischen Brocken nur unter Mitarbeit des Archäologen ein Bild der zeitlichen und räumlichen Ausbreitung der Kulturpflanzen gewonnen werden kann.

### 3. Datierung.

Das schwierigste Problem ist aber die Datierung. Hier lassen sich ähnlich wie bei den biologischen Methoden drei durch bestimmte neue Entdeckungen eingeleitete Perioden unterscheiden.

I. — 1925

II. ab 1925

III. ab 1948

Die I. Periode bis etwa 1925 kann man als die historisch-archäologische bezeichnen; dabei ist zu unterscheiden zwischen Datierungen im Orient und im europäischen Raum.

a) im Orient ist die Datierung abhängig vom Stand der historischen Forschung; seit 1905 auf EDUARD MEYER's Geschichte des Altertums fussend, sind die Datierungen sehr alt gesetzt.

Der Beginn der ackerbaulichen Kulturen im Orient, speziell in Ägypten, galt demnach fast unbestritten allen andern zeitlich vorangehend. Die Datierungen, wenn auch mit Unsicherheiten belastet, galten als absolut.

b) im europäischen Raum sind die Datierungen zunächst nur rein typologisch — also nur relativ — gewonnen — eine Zeitfolge wurde aus der Höhe der Stilentwicklung der Keramik abgelesen; erst allmählich setzte sich eine stratigraphische Beurteilung durch (VOUGA 1929); auch diese führt naturgemäss nur zu relativen Datierungen. Die Bandkeramik, wie die nordischen Megalithkulturen zeigen sich im Besitz der gleichen Kulturpflanzen wie die zuerst bekannt gewordene Pfahlbaukultur. Für eine Synchronisierung untereinander oder mit den Orient-Kulturen fehlen die Möglichkeiten.

Die II. Periode, die ich die geologisch-archäologische nennen möchte, setzt um 1925 mit der Anwendung der LAGERHEIM-VON POST-schen Methode der Pollenanalyse auf archäologische Funde ein, erstmalig durch ERDTMAN in Schweden hierfür ausgewertet. Sie ist bis heute methodisch laufend vervollkommenet und hat zu einer guten Datierung relativ zur Waldgeschichte geführt. Ab 1923 hat FIRBAS die Ergebnisse zu einer Waldgeschichte von Mitteleuropa ausgearbeitet, in der die Kulturpflanzenfunde eingefügt sind.

Nach Eichung von Waldprofilen mit typologisch bestimmten Funden ist die Methode nunmehr zur weiteren Datierung geeignet (RYTZ, 1930). Zunächst wurde nur Baumpollen berücksichtigt; die Einbeziehung des Nichtbaumpollens, darunter wichtige Unkrautpollen, führt zur Beurteilung der landschaftlichen Umgebung der Kulturfunde und hat zum Nachweis von Rodung (IVERSEN 1941) bei der Besiedelung durch den Menschen geführt.

1937 wird durch FIRBAS und MÜLLER der Getreidepollen mit einbezogen; und in dieser Form wird die Pollenanalyse für die Geschichte der Kulturpflanzen bis heute gehandhabt.

Eine Ergänzung hat sie durch Einbeziehung der Diatomeenflora durch HALDEN 1929 für Siedlungsanlagen an Binnensee- und Meeresufer gefunden.

Endlich kann auch die Höhe des Phosphatgehaltes im Boden über Lage und Ausdehnung menschlicher Siedlungen Auskunft geben. Diese Methoden (a) finden im europäischen Raum Verwendung, wo seit Mitte der zwanziger Jahre eine erhöhte Ausgrabungstätigkeit festzustellen ist.

b) Etwa gleichzeitig macht sich ein Aufschwung in der historischen Orientforschung in einer Revision der Datierungen bemerkbar, die z. T. sehr wesentlich jünger angesetzt werden und zu einer Synchronisierung der mesopotamischen und ägyptischen Frühgeschichte geführt haben. (Letzte Darstellung bei SCHARFF und MOORTGAT, 1950.) Von da aus haben die Zeitschätzungen der Vorgeschichte grössere Sicherheit gewonnen, das macht sich bei der Datierung der gleichzeitig um 1930 erhöht einsetzenden Ausgrabungstätigkeit in Ägypten und Vorderasien geltend, die reiches Kulturpflanzenmaterial zu Tage gefördert hat. Diese Datierungen sind für die Bestimmung der Wanderungswege der Kulturpflanzen von Bedeutung. Heute stehen im Orient englische, französische und amerikanische Ausgrabungen im Vordergrund. Die deutschen Arbeiten in Mesopotamien und Anatolien konnten erst in jüngster Zeit wieder aufgenommen werden. Diese zweite historisch-archäologische Periode setzt sich also bis in die Gegenwart fort.

Eine III. Periode ist bestimmt durch die Bemühung um eine absolute Zeitbestimmung, die sich von Europa über die ganze Erde erstrecken kann. Sie entwickelt nacheinander I. eine Geochronologie in der seit 1884 aufgebauten Warvenmethode de Geers. Sie beruht auf der Bildung der durch jahreszeitlich bestimmte Sedimente an den Rückzugsrändern des nordischen Inlandeises entstandenen Bändertone, mit de Geer als „Warven“ bezeichnet. Sie erlaubt eine Verknüpfung mit der pollenanalytisch relativ datierten Waldgeschichte und einen An-

schluss an die heutige Zeit; sie beginnt um 1925 sich für die Bestimmung der Kulturpflanzenfunde auszuwirken.

2. eine Dendrochronologie oder Jahresringchronologie, seit 1909 von DOUGLAS in Amerika an Sequoien ausgearbeitet; 1937 von GLOCK, DOUGLAS a. PEARSON eingehend beschrieben. Aus der regelmässigen Wiederkehr bestimmter Folgen von Jahresringbreiten lässt sich auf periodische Klimaschwankungen schliessen. Andererseits ermöglicht die Einmaligkeit mancher Folgen innerhalb der Klimaperioden eine Synchronisierung an verschiedenen Orten. Diese Methode kann durch Einordnung von Holzfunden in prähistorischen Siedlungen zur absoluten Zeitbestimmung derselben verwendet werden.

Sie ist für die europäischen Verhältnisse von HUBER (seit 1941) und MÜLLER-STOLL ausgearbeitet und hat bereits eine weitgehend zusammenhängende Chronologie von der Jetztzeit rückwärts bis zur Bronzezeit ergeben (Vergl. auch E. HULT-DE GEER.).

3. eine Limnochronologie; in ähnlicher Weise auf Grund der limnischen Jahresschichtungen in ruhigen Gewässern aufgestellt, in jüngster Zeit (1944) von WELTEN für die Schweiz (Faulenseemoos bei Spiez) ausgearbeitet; sie kann indessen noch nicht als vollständig angesehen werden, verspricht aber bei Erweiterung der Untersuchungen gesicherte absolute Daten auch bei Inlandsiedlungen.

Endlich tritt als 4. und letzte die Radiochronologie; sie ist 1948 durch LIBBY aufgestellt und als Radiocarbonmethode bezeichnet. Sie beruht auf der Bestimmung des Gehaltes der organischen Körper an Radiokarbon, dem radioaktiven Isotop  $C^{14}$  des Kohlenstoffs, auf Grund der bekannten Halbwertszeit von  $C^{14}$  (heute auf 5568  $\pm$  30 Jahre festgestellt). Da beim Absterben des organischen Objektes die Absorption des  $CO_2$  der Luft aufhört, deren Gehalt an  $C^{14}$  als konstant festgestellt wurde, lässt sich das absolute Alter des Objektes aus der noch vorhandenen Menge von radioaktivem Kohlenstoff berechnen. Im Gegensatz also zu den vorigen Methoden, welche das Alter des Substrates, in dem der Kulturfund eingebettet lag, feststellen, wird hier das Alter des Objektes selbst bestimmt.

Die Werte, bis zu 20.000 Jahren mit ausreichender Genauigkeit, lassen für die Zeiten, die für die Anfänge des Ackerbaues und seine erste Verbreitung in Frage kommen, noch eine geringere Schwankung erwünschen. Ein  $\pm$  von 250–300 Jahren, d. h. Spannen von 500–600 Jahren können bei Wanderungen von Volksstämmen — oder von Kulturgütern von Stamm zu Stamm nicht zu Synchronisierungen von Kulturfolgen verwendet werden. Es fehlt uns aber, um ein Beispiel zu nennen, der zeit-

liche Zusammenhang der orientalischen, besonders der vorderasiatischen, aber auch der ägyptischen Kulturen mit den europäischen, der etwa die Frage, ob und wie die Bandkeramiker die Überbringer des ersten Getreides und des ersten Ackerbaues nach Mitteleuropa sind, entscheiden könnte.

### Chronologie der Ergebnisse.

Wir kehren damit zu den eingangs skizzierten Perioden zurück und fassen die Ergebnisse der beiden ersten Perioden bis 1900 zusammen, weil sie methodisch übereinstimmen: die Anregung, die von den genannten Arbeiten ausging, musste sich erst auswirken. Die Zeit vor DE CANDOLLE hatte als Quelle für die Geschichte der Kulturpflanzen auf die antiken naturwissenschaftlichen Schriftsteller zurückgegriffen, vor allem auf Aristoteles, Theophrast, Plinius und Dioscorides. Die Kritik, die DE CANDOLLE schon 1855 an der Zuverlässigkeit dieser Berichte unter Einführung biologischer Methoden übte, zeigte, dass diese Quellen unsicher sind, die Pfahlbautenfunde bewiesen, dass sie längst nicht weit genug zurückgreifen. Doch behalten sie einen gewissen Wert für das weitere Schicksal der Kulturpflanzen in historischer Zeit. LENZ hatte bereits 1859 alles zusammengestellt, was über die Botanik der alten Griechen und Römer bekannt war, dabei sind auch die Kulturpflanzen mitbehandelt.

Den ersten Pfahlbautenberichten aus der Schweiz folgt eine rege Ausgrabungstätigkeit an Land-, See- und Moorsiedlungen von Mitteleuropa bis zu den Balkanländern und Ungarn, die alle Kulturpflanzenreste liefern, aus Pfahlbauten besonders am Nordrand der Alpen.

Im Orient gehen die Bestimmungen älterer Sammlungen und Deutungen von Inschriften und Bildern neben denen neuer Ausgrabungen her.

Amerika liefert in Ankon die ersten reichen prähistorischen Funde (1880), SCHLIEMANN's Troja eröffnet die Reihe der vorderasiatischen. Für Mesopotamien ist man auf Bilder und Inschriften angewiesen; für China ersetzen altchinesische Schriften (BRETSCHNEIDER 1870) substantielles Material.

Diese Untersuchungen lehren, dass die Kulturen des Orients bis nach China und der älteste Ackerbau in Europa vom Neolithicum an im wesentlichen auf den gleichen Kulturpflanzen aufgebaut sind, wenn auch noch wenig spezifisch unterschieden: Gerste und Weizen, besonders Emmer (für das klassische Altertum ausschliesslich), Hirse, einige Leguminosen: Erbse, Saubohne, Linse, (*Pisum*, *Vicia faba*, *Lens*) — Lein. Roggen- und



Haferarten treten später auf als die anderen Getreide und fehlen dem Orient. Die Frage des Spelzes bleibt ungeklärt. In Amerika werden neben Mais auch Bohnen (*Phaseolus*) und Kürbis als indigen festgestellt.

Neben DE CANDOLLE's eingehender Behandlung von 240 Kulturpflanzen (1883), stehen monographische Einzelstudien über Lein, Weizen und Tulpe, Erdbeere, Getreide, amerikanische Kulturpflanzen u. a. Die Frage entsteht: wie diese Kulturen zeitlich und kulturell in Zusammenhang stehen, welches die Wanderwege der Kulturpflanzen gewesen sind.

Für den Orient steht die Beziehung zwischen Mesopotamien und Ägypten zur Diskussion. Die Antwort fällt auf historischer Grundlage zu Gunsten Ägyptens als ältester und gebender Kultur; der Stand der damaligen Kenntnisse ist durch Eduard Meyer repräsentiert.

Da für Europa historisch absolute Daten fehlen, liegt die Beantwortung auf Grund der Keramikstile bei der Ethnologie. In Mitteleuropa weisen diese Ergebnisse alle auf einen Beginn des Ackerbaues (mit der Tierzucht) im Neolithicum. (Zusammenstellung dieser Funde für Mitteleuropa bei NEUWEILER 1905).

Dass auch die Linguistik hierbei erfolgreich herangezogen werden kann, hat DE CANDOLLE schon 1855 betont. Mit ihrer Hilfe geht Viktor Hehn der Frage nach; sein grosses kulturgeschichtliches Werk sucht die Vermittler zwischen Orient und Occident und weist die Zusammenhänge für über 60 der wichtigsten Kulturpflanzen und Haustiere nach. Wenn auch viele Einzelheiten in HEHN's Werk schon zu Ende des Jahrhunderts durch neue Forschungen überholt sind (vergl. hierzu die Anmerkungen von A. ENGLER und O. SCHRADER für die VI. Afl. 1894), so hat er doch den grossen Zusammenhang und die wesentliche Ost-Westwanderung der auf Ackerbau und Viehzucht beruhenden Kulturen deutlich gemacht.

Von DARWIN's Lehren hat sich die Selektionstheorie bis 1900 noch wenig direkt ausgewirkt. Die Frage nach dem Zusammenhang zwischen Wild- und Kulturform wird geographisch-morphologisch bearbeitet, stärker unter der Anregung von DE CANDOLLE stehend. Archäologisch fällt ferner in diese zweite Periode die erste Ausnutzung der Kornabdrücke in Scherben durch SARAuw, die indessen als Methode in Vergessenheit geriet. Doch finden seine Resultate Verwendung bei HOOPS (1905) in einer ersten Zusammenstellung prähistorischer Kulturpflanzenfunde.

Als Nachklang der Methodik der ersten beiden Perioden ist die im zweiten Jahrzehnt einsetzende sehr intensive Arbeit von AUGUST SCHULZ zu nennen, die 1911 zur Aufstellung der bis heute gültigen drei Weizenreihen führt. Er hat fortlaufend mit morphologisch-geographischen Methoden archäologische Funde Europas und Ägyptens botanisch



bearbeitet und kulturhistorisch gedeutet. Auch WITTMACK und SCHWEINFURTH arbeiten weiter im gleichen Sinne. Als einschneidendes Ergebnis ist die auf Anregung Schweinfurths und Körnickes zurückgehende Entdeckung des wilden Emmers in Palästina 1906 durch AARONSOHN zu nennen.

Die geographisch-morphologische Methode greift die V. Periode dann wieder auf.

Die linguistische Bearbeitung des Problems ist in späterer Zeit durch HROZNY's babylonische Kulturpflanzenstudien (1914) vertreten; dann tritt die Methode zurück. Erst 1944 bearbeitet JASNY die Weizen des klassischen Altertums erneut von sprachlich-historischer Seite her. Doch haben spätere Forscher etwaige sprachliche Indizien für ethnographische Beziehungen ausgewertet. (Hindukusch-Expedition u. a.).

Die III. Periode, die mendelistische (1900–1918) hat von vornherein reiche Früchte für die Geschichte der Kulturpflanzen gebracht dank der Methodik, welche sich in der zweiten Hälfte der 19. Jahrhunderts mit VILMORIN's Prinzip der Beurteilung nach der Nachkommenschaft in der Züchtung durchgesetzt hatte. Indem sie dem Mendel-experiment die reinen Linien zur Verfügung stellte, fand diese nun schon bewährte Züchtungsmethode ihre theoretische Erklärung. So kam es, dass die wichtigsten Kulturpflanzen, Getreide und Leguminosen, sogleich die Objekte für theoretisch in dieser Periode im Vordergrund stehende Probleme lieferten, für die Fragen nach den Ursachen von Variabilität und Anpassung. Als Ursachen der Variabilität werden Kreuzung und Mutation erkannt — Kreuzung als experimentelle Methode, (BIFON, NILSSON-EHLE, KAJANUS, TAMMES), wobei dann die aus dem 18. Jahrhundert bekannten, aber nicht verstandenen Resultate der Art- und Gattungskreuzungen für die Phylogenie der Kulturpflanzen, speziell der Getreide herangezogen werden, (SUTTON, 1908–14, v. TSCHERMAK, 1914, MALINOWSKI, 1914/18, PERCIVAL, 1921).

In den Mutationsversuchen wird auch die reine Beobachtung in das Experiment einbezogen. JOHANNSEN erkennt, dass die Kulturpflanzen-„sorten“ Populationen genetisch reiner Linien sind.

Um Mutationen von Kreuzungsergebnissen unterscheiden zu können, wird die reine Linie als Ausgangspunkt jedes exakten Versuches verlangt (BAUR). Das führt zur Anlage von Sortimenten, in Russland seit 1905 von ROBERT REGEL für Gerste und Weizen aufgebaut, von Baur seit 1911 als erstes in Deutschland zu wissenschaftlichen Zwecken angelegt, unter Einbeziehung der wilden Arten — heute überall eine Selbstverständlich-

keit und das Ausgangsmaterial liefernd, wo es gilt die Variabilität einer Sippe (Gattung, Art, Sorte) genetisch zu erfassen. Damit knüpft die Methodik an die systematisch-morphologische Methode der früheren Perioden an (KÖRNICKE, 1885), besonders in der russischen Schule geübt (Flaksberger u. a.).

Das zweite Hauptproblem dieser Periode ist die Anpassung; hier kommt DARWIN's Selektionstheorie zur vollen Auswirkung — im Neodarwinismus wird in Verbindung von Mutation, Kreuzung, Selektion eine Erklärung für die Evolution gesetzt. Hierhinein fällt die Entdeckung des wilden Emmers, neben dem schon lange bekannten Einkorn, was die Darwinsche Frage nach der Entstehung der Kulturform aus der Wildform dem Experiment zugänglich macht. Man versteht das Verschwinden der spezifischen Wildmerkmale als spontane Mutation, gefolgt von Selektion durch den sesshaft werdenden Menschen. (Nachweis der mendelnden Brüchigkeit bei Gerste — v. UBISCH, SCHIEMANN, 1915–21, bei Weizen — LOVE a. CRAIG, 1919).

Im Zusammenhang mit NILSSON-EHLE's Nachweis der mendelnden Vererbung auch von physiologischen Merkmalen (Winterfestigkeit, Rostresistenz) wird der Wert der Landsorten in ihrer ausserordentlichen Anpassung erkannt. Als praktische Folge (Aufruf v. TSCHERMAK und BAUR, 1913) werden sie gesammelt, und in ihre Linien aufgelöst, in die Sortimente aufgenommen. Experimentell bringt diese Periode eine Beschränkung des Forschers auf ein Versuchsobjekt, um der Forderung genauester Beobachtung gerecht zu werden; das theoretische Resultat ist die Lehre von den Kleinmutationen als Evolutionsschritten. (BAUR).

Nachklang: Diese Methodik klingt nach in den zur Genanalyse durchgeführten Kreuzungsanalysen, ausgedehnt auf alle Kulturpflanzen, auch das Obst — mit reichen Resultaten in den zwanziger Jahren. Vavilov (1922) knüpft mit seinen „homologen Reihen“ an DARWIN's Begriff der „Parallelvariationen“ an. Dies führt zur Entdeckung der „süssen“ Lupine (BAUR, v. SENGBUSCH). Endlich bringt TURESSON neue Gesichtspunkte für die Anpassung mit der Einführung der Ökotypen-Ökospecies (1922) in die Systematik. ZINGER, THELLUNG, SINSKAJA weisen Kulturpflanzeigenschaften bei Unkräutern als Selektionswirkung nach.

Archäologisch bringt die Zeit von 1900 bis 1918 in den exakten Bestimmungsarbeiten von Schulz, WITTMACK, NEUWEILER, NETOLITZKY eine Einengung der allgemeinen Angaben über die Getreide. — Die Verbreitung von Einkorn im Neolithicum Europas und in Anatolien (Troja), sein Fehlen im orientalisch-semitischen Kulturkreis, wo aus-

schliesslich Emmer nachgewiesen wurden, wird deutlich. *Triticum Spelta* erweist sich auf das Oberrheingebiet beschränkt, erst in der Bronzezeit beginnend. Damit taucht das *Spelta*-Problem auf, das gleichzeitig genetisch an den Speltoidmutanten angegriffen wird. Schulz rollt die Frage der Nackt- und Spelzweizen und -gersten für Ägypten auf; er geht auch der weiteren Geschichte der Getreide durch das historische Altertum bis zu seinem heutigen Vorkommen nach. — Die Ableitung des Roggens, der erst seit der Eisenzeit im östlichen Mitteleuropa wirklich gesichert ist, von *Secale montanum* var. *anatolicum*, bleibt hypothetisch.

#### IV. Die cytogenetische Periode, 1918 eingeleitet durch die Entdeckung der Polyploidie des Weizens.

Diese löst zunächst die Feststellung der Chromosomenzahlen bei allen genetisch bearbeiteten Kulturpflanzen aus, die erkennen lässt, dass die Kulturpflanzen vielfach in den höheren Polyploidiestufen polyploider Reihen liegen. Unter dem Eindruck von DE VRIES' *gigas*-Mutante wird der diploide Zustand als primitiv angesehen und der höhere Ertrag, die grösseren Dimensionen, sowie die grössere Variabilität der Kulturpflanzen gegenüber ihren wilden Verwandten mit der Polyploidie in Zusammenhang gebracht. Man sucht mithin die Ur- oder Stammform unter den Diploiden. SCHULZ' Gruppierung der Weizen erweist sich als ein Stammbaum.

1932 konnte SCHIEMANN die Chromosomenzahlen der wichtigsten Kulturpflanzen zusammenstellen, die DARLINGTON und JANAKI 1945 auf breiter Basis zu einem „Chromosomenatlas der Kulturpflanzen“ ergänzt haben.

Die IV. Periode wurde zusammenfassend charakterisiert durch den Satz: „Als grundlegende Methode zur Analyse der phylogenetischen Zusammenhänge bleibt die Cytogenetik“ — sie ist es, angewandt auf alle Kulturpflanzen, geblieben bis heute. Wir bringen im folgenden die wichtigsten Resultate zeitlich geordnet, bis neue Impulse in die Arbeit eingreifen; die zwanziger Jahre sind besonders fruchtbar gewesen.

Die bisher nur genetisch ausgewerteten Art- und Gattungsbastarde werden cytologisch geprüft — seit 1919 steht KIHARA hier mit seiner Schule für Getreide, Weizen, Hafer in vorderster Reihe.

Wichtige Arbeiten im gleichen Sinne werden an *Nicotiana* und *Solanum* durchgeführt, an Obst und Leguminosen, in Amerika wird an der Analyse *Euchlaena-Tripsacum-Zea* gearbeitet.

1921 weist SAX die Homologie eines Genoms von *Aegilops cylindrica* mit *Triticum vulgare* nach. Damit wird die morphologisch — über

Spelta — gewonnene Ansicht, dass die hexaploiden Weizen ein *Aegilops*-genom besitzen, zum festen Bestandteil aller Hypothesen zur Phylogenie des Weizens, und die Bindungen in der Meiosis gewinnen phylogenetische Bedeutung.

1924 stellt KIHARA an den pentaploiden Weizenbastarden in den Vermehrungs- und Verminderungsreihen teilweise fertiler Bastarde die Auswirkung der gestörten Reduktionsteilung auf die Fertilität und Sterilität und ihre Bedeutung für die Evolution fest. Es folgt eine fortlaufende Untersuchungsreihe der Japaner an penta- und triploiden Weizenbastarden und parallel dazu am Hafer bis zu den Schlusszusammenfassungen 1940 ff.

1926 gibt ROSENBERG in der semiheterotypischen Teilung eine Erklärung für viele Fälle der Chromosomenverdoppelung. Im gleichen Jahre berichten v. TSCHERMAK und BLEIER über die ersten *Aegilotriticum*-Amphidiploide. Die Triticeengattungen *Triticum*, *Secale*, *Agropyrum*, *Aegilops*, *Haynaldia* werden cytogenetisch auf ihre Verwandtschaft geprüft (v. TSCHERMAK, OEHLER, KATTERMANN, KIHARA und Mitarbeiter, PERCIVAL u. a.).

Allein die Weizen-Roggen und Weizen-*Aegilops*-Bastarde zeitigen eine umfangreiche internationale Literatur. Man sucht den Ursprung der drei Weizengenome (AASE, 1930).

Auch die Chromosomenmorphologie wird einbezogen (KAGAWA, 1927), die von MCCLINTOCK zuerst für Mais ausgearbeitet ist und heute erneut im Vordergrund des Interesses steht.

Eine weitere Reihe von Kulturpflanzen wird als amphidiploid erkannt (Pflaume, Tabak, Raps u. a.).

1939 bringt SEARS eine neue cytogenetische Methode in der Chromosomenanalyse des Weizens mittels Nulli- und Tetrasomics. Sie ermöglicht die bei hochchromosomigen Arten schwierige Lokalisation der Gene und hat durch die Lokalisation der Gene im B- und D-Genom für die noch nicht voll geklärte Entstehung der hexaploiden Saatweizen Bedeutung.

1946 wird in *Aegilops squarrosa* der Spender des D-Genoms gefunden (McFADDEN-SEARS, KIHARA).

V. Periode. Während diese Arbeiten ununterbrochen bis heute fortgesetzt werden, bricht 1926 mit VAVILOV's russisch-englischem Bericht: *Origin of Cultivated Plants* und dem entsprechenden Vortrag auf dem VII. Internationalen Genetikerkongress in Berlin 1927 durch die von ihm entwickelte Genzentren-Theorie eine neue Periode an; sie ist gekennzeichnet durch die Verknüpfung der alten systematisch-morphologischen



Methode (Periode I und II) mit der Genetik (Periode III), von VAVILOV als systematisch- (oder morphologisch-) geographische Differentialmethode bezeichnet; bald auch mit der Cytogenetik.

In ihrer Vorgeschichte stehen DE CANDOLLE's geographische Analyse, BATESON's Variabilitätsstudien, BAUR's Mutationsforschung, JOHANNSEN's Lehre von den reinen Linien, NILSSON-EHLE's Griff auf die Land-sorten und als Material das grosse Sortiment ROBERT REGELS auf den edaphisch verschiedenen landwirtschaftlichen Stationen Russlands. VAVILOV's Tat ist die grosszügig angelegte Erforschung des Kulturpflanzenbestandes der alten und der neuen Welt, zunächst in der gemässigten und subtropischen Zone. Das Ergebnis ist die Erfassung des Materiales in seiner Mannigfaltigkeit, seiner Häufung in bestimmten Arealen, den Genzentren, die Theorie über den Ursprung der Kulturpflanzen: die Genzentrentheorie, wie über den Ursprung der landwirtschaftlichen Kulturen (Berge, nicht Stromtäler!).

Die Abhandlung von 1926 bringt zu diesen theoretischen Vorstellungen für die wichtigsten altweltlichen Kulturpflanzen schon die Einzelresultate, aus denen sie gewonnen sind.

Auch in der Berücksichtigung von Geschichte und Ethnologie nimmt VAVILOV De Candollesche Gedankengänge auf. —

Die Lehre von den primären und sekundären Kulturpflanzen hat ihre Vorläufer in den kulturgeschichtlichen Studien von BROCKMANN-JEROSCH (1917/25), ENGELBRECHT (1916/17), MAURIZIO (–1927). Das wichtigste Resultat ist die Feststellung, dass der Roggen als Unkraut im Weizen in die Kultur übernommen ist, der Prototyp für viele andere Kulturpflanzen. Dazu kommt die für die Weiterentwicklung der Kulturpflanzen wichtige Erkenntnis: die Genzentren sind eine Genreserve, die mit den Methoden der Cytogenetik für die rezente Landwirtschaft nutzbar gemacht werden kann.

Die Anregung ging in die ganze Welt als Impuls

1) für Sammelexpeditionen; ihre wichtigsten Entdeckungen für die Geschichte der Kulturpflanzen sind

a) die Erfassung des Formenreichtums an tetraploiden Weizen in Transkaukasien, besonders durch russische Forscher.

b) Die Entdeckung des Wildroggens, *Secale ancestrale*, in Anatolien 1928 durch ZHUKOVSKY.

c) die Entdeckung der 6-zeiligen Wildgerste, der hypothetisch geforderten Stammform der Kulturgersten durch ÅBERG, 1938, und anschliessend der brüchigen Intermedium-Gersten (SCHIEMANN, 1951), sowie der Primitivweizen und -Gersten (BRÜCHER, 1950), alle in Ost-Tibet.



Diese Entdeckungen haben zu einer Revision der Genzentrentheorie geführt, Abessinien und das Hindukuschgebiet werden als Sekundärzentren angesehen, Transkaukasien als das Primär (=Entstehungs-)zentrum der tetraploiden und hexaploiden Weizen (SCHIEMANN, 1939).

d) die Sammlung von Wild- und Primitivkartoffeln in Südamerika (JUZEPUK und BUKASOV, 1929, BAUR-SCHICK, 1930, HAWKES, 1941) und die Feststellung, dass die Kartoffeln Europas von *Solanum andigenum* abzuleiten sind.

e) in letzter Zeit die Erfassung der alten Indianerkulturen von Mais in Süd- und Mittelamerika und in Mexiko, welche die Entwicklung des Maises weitgehend geklärt hat. (MANGELSDORF u. Mitarbeiter, u. a.)

2) für monographische Bearbeitung der einzelnen Kulturpflanzen nach obigen Methoden (vergl. bes. Bull. of applied Botany, Der Züchter, J. of Heredity).

Viele Einzelheiten in folgenden Zusammenfassungen:

SCHIEMANN: Entstehung der Kulturpflanzen 1932 und 1943, Flora of Cultivated Plants herausgegeben von VAVILOV, Bd. I, 1935 ff., unvollendet (russisch).

BERTSCH: Geschichte unserer Kulturpflanzen 1947.

ZHUKOVSKY: Kulturpflanzen und ihre Verwandten 1950 (russisch).

Der archäologische Beitrag zur V. Periode (1925–37) ist reich in Folge einer sehr regen Ausgrabungstätigkeit, sowohl im Orient, wie in Mittel- und Nordeuropa vom Alpenrand bis nach Skandinavien, die im grossen und ganzen den Bestand an Kulturpflanzen durch mannigfache z. T. sehr umfangreiche Funde bestätigt. In Ägypten erschliesst sich die prädynastische Zeit im Nildelta bis ins Neolithicum zurück. Die pflanzengeographischen Anregungen VAVILOV's, welche die Ursprungsfrage von Weizen und Gerste zur Diskussion gestellt hatten, erhielten von hier neues Licht. Entgegen VAVILOV's Annahme von einem Ursprung der Emmerkultur in Abessinien und Wanderung nach Norden, konnte deshalb schon 1931 die Arbeitshypothese aufgestellt werden, dass die Entwicklung des Emmers und der Emmerkultur den umgekehrten Weg, von Vorderasien, der Heimat von *Triticum dicoccoides* (Persien bis Palästina) nach Süden gegangen ist, Ägypten also von Norden erreicht hat, lange vor dem ägyptischen und mesopotamischen frühhistorischen Stadtkulturen (vergl. SCHIEMANN 1932, S. 101, 1943, S. 510 ff.).

Gleichzeitig hat die Pollenanalyse mit den ihr angeschlossenen Methoden für Europa das nacheiszeitliche Landschaftsbild in seiner zeitlichen Umwandlung entworfen und damit den Rahmen für die in unserm Zusammenhang am meisten interessierende Epoche, die Einwanderung

der Ackerbaukulturen mit dem Menschen geschaffen. — Daran schliesst sich eine rege ethnologische Arbeit; Pflug, Hackbau, Wirtschaftsform — von HAHN schon 1909 behandelt — werden neu erörtert (WERTH); die zeitliche Einordnung in Vorneolithische Kulturen steht zur Diskussion. — Die Wiederaufnahme der Bestimmung nach Abdrücken in Gefässscherben (JESSEN-HELBÆK) erweitert besonders die Kenntnisse des Ackerbaues nach Nord- und Westeuropa hin und lässt auch seinen geschichtlichen Verlauf erkennen.

Die VI. Periode bringt mit der Einführung der Colchizinmethode 1937 als interessantestes Ergebnis für die Phylogenie der Getreide die Synthese von *Triticum spelta* als Amphidiploid *Triticum dicoccoides* × *Aegilops squarrosa* durch MCFADDEN-SEARS, welche die Entstehung der hexaploiden Weizen neu belebt, indem sie zwar nicht eine Lösung bringt, aber neue Probleme aufwirft, die der Bearbeitung zugänglich sind.

Die theoretischen Fragen der Auto- und Allopolidie werden aufs neue experimentell angegriffen. Eine grosse Anzahl von Kulturpflanzen wird als amphidiploid erkannt; die Herstellung hochpolyploider Pflanzen gewinnt praktische Bedeutung in Land- und Forstwirtschaft und Gartenbau — d. h. in der neuzeitlichen Weiterentwicklung der Kulturpflanzen.

Auch die künstliche Auslösung von Gen- und Chromosomenmutationen durch Bestrahlung u. a. beginnt für die Entstehung der Kulturpflanzen Früchte zu tragen. Umschläge von Zwei- zu Mehrzeiligkeit bei Gersten werden für die Frage herangezogen, welche der beiden Formen die primitivere ist. (STUBBE u. BANDLOW, 1947, FREISLEBEN u. LEIN, 1944).

Auch die Speltafrage ist mittels Strahlenmutanten in Verbindung mit den natürlichen Speltoidmutanten erneut beleuchtet worden (MACKEY 1954).

1939 gelingt es SEARS mit der Methode der Nulli- und Tetrasomics das D-Genom in *Triticum aestivum* (= *vulgare*) zu lokalisieren.

Auch archäologisch ist das Jahr 1937 einschneidend. Die Einführung des Getreide-, wenig später des Unkrautpollens als Siedlungsanzeiger in die Pollenanalyse entscheidet die Diskussion über mesolithischen, ja selbst paläolithischen Ackerbau — heute kann der Beginn in Europa im Neolithicum als gesichert gelten. Präzise gestellt wird die Frage nach dem ersten Auftreten der Saatweizen (*Triticum aestivum* — *vulgare*) durch BERTSCH. Da *Triticum compactum*, der Binkelweizen für die neolithischen Kulturen charakteristisch ist, hängt das Problem mit der Entstehung der hexaploiden Nacktweizen zusammen, zu dem die

Hypothese von MCFADDEN-SEARS, 1944, ganz neue Fragen aufgeworfen hat.

Wenn mit der Radiokarbonmethode für die Chronologie ein neuer Abschnitt begonnen hat, eine neue, VII. Periode, so trägt eine neue Welle von Ausgrabungen ihr reiches Material zu: 1948 wirft TÄCKHOLM mit dem Getreide aus el Omari die Frage des Einkorns für Ägypten auf. — 1953/54 wird sie in alter Weise beantwortet (HELBÆK, SCHIEMANN), wenn auch die letzte Entscheidung noch aussteht. — Iraq und Syrien liefern in vorkeramischen Kulturen (radiokarbon-datiert) den wilden Getreidegräsern nahestehende Weizen und Gersten — entsprechend den 1931 entwickelten Hypothesen.

Roggen, bisher nur aus Bronze- und Eisenzeit bekannt, wird in Wien aus dem Neolithicum beschrieben; der Spelz, der am Oberrhein in der Bronzezeit lokal begrenzt auftritt, wird für Württemberg, mit Vorbehalt auch für Dänemark, als neolithisch angegeben — während gleichzeitig durch die genetische Analyse die Möglichkeit seiner Entstehung auf Grund einer Radiomutation erörtert wird, und damit im Sinne einer Widerlegung der MCFADDEN-SEARS-schen Theorie ein Beitrag gebracht ist.

In Amerika bringt die Ausgrabung der „Bat Cave“ den ersten Abschluss einer langjährigen Arbeit nach den verschiedensten Methoden zur Aufklärung der Herkunft des Maises. Zytogenetische Analyse von Art- und Gattungskreuzungen, Sammlung der alten Indianerkulturstämme und ihre Einbeziehung in diese Analyse, historische und archäologische Studien und endlich botanisch-morphologische und entwicklungsphysiologische Analyse der ♀ und ♂ Infloreszenz tragen die Bausteine zusammen, die ein ganz neues Verständnis für die Natur und Geschichte des Maises ergeben. (MANGELSDORF u. a.)

Man darf wohl sagen, dass in keiner Zeit die archäologischen, genetischen, geobotanischen und pflanzengeographischen Fragen so ineinander gegriffen haben, wie seit den letzten zehn Jahren.

Dieser Überblick hat deutlich gemacht, worauf im Anfang hingewiesen wurde, dass jede neue Periode zwar durch eine neue Methode einen Impuls bekam, dass aber die Methodik der früheren Zeit damit nicht entwertet wurde, sondern vielmehr bereichert. So stehen dem Kulturpflanzenforscher heute die verschiedensten Methoden zur Verfügung, um an eine Einzelfrage heranzugehen. Bei der Schwierigkeit der Deutung phylogenetischer Fragen, die in längst vergangene Zeiten zurückgehen und denen vielfach nur lückenhaftes Material zur Verfügung steht, ist

die Möglichkeit von verschiedenen Seiten an ein Problem heranzugehen, von unschätzbarem Wert.

Darum drängt die Kulturpflanzenforschung zu einer engen Zusammenarbeit so weit auseinander liegender Disziplinen, wie Archäologie und Geologie und innerhalb der Biologie Systematik und Morphologie, Genetik, Pollenanalyse und Biophysik. Fruchtbar kann die Arbeit nur werden bei Anwendung aller bewährten Methoden, um bei der Mehrdeutigkeit der Ergebnisse die Möglichkeiten der Deutung auf das Mindestmaß einzuschränken, in freiem Austausch auf internationaler Basis.

### Literatur.

Eine vollständige Literaturliste zur Geschichte der Kulturpflanzen — heute schon ein schwieriges Unternehmen — ist einer späteren Arbeit vorbehalten. Die Literatur bis 1932, 1943 und 1949 findet sich bei:

SCHIAMANN, E., 1932: Entstehung der Kulturpflanzen. Handb. d. Vererbundswiss. III L.

— 1943: Entstehung der Kulturpflanzen in: Ergebnisse d. Biologie 19.

STUBBE, H., 1949: Genetisch-pflanzenzüchterische Bibliographie 1939–46: (1947) Sonderheft 1948 d. „Züchter“.

für prähistorische Funde bei:

FIRBAS, F., 1949: Waldgeschichte Mitteleuropas I.

— 1952: Waldgeschichte Mitteleuropas II, Fischer, Jena.

TÄCKHOLM, V. L. u. DRAR, M.: Flora of Egypt I 1941, II 1950.

Grössere neue Darstellungen des Gesamtgebietes sind:

BERTSCH, K. u. F., 1947: Geschichte unserer Kulturpflanzen. Wiss. Verlagsges. Stuttgart.

ZHUKOVSKY, P. M., 1950: Kulturpflanzen und ihre Verwandten (russ.) Verlag Moskau.

Flora of Cultivated Plants (russ.) herausgegeben ab Bd. I 1935 von Vavilov — im Erscheinen; z. Z. Bd. I, II, IV, V, XIII.

HATT, G., 1937: Landbrug i Danmarks oldtid. Copenhagen.

RYTZ, W., 1949: Die Pflanzenwelt. Botanische Wege und Ziele in der Urgeschichtsforschung der Schweiz. Urgesch. d. Schweiz I.

### Einzelfragen betreffend

A) biologisch.

AASE, H. C., 1946: Cytology of Cereals. Botan. Reviews 12.

SEARS, E. R., 1939: Cytogenetic Studies with polyploid species of wheat. I. Genetics 24.

— 1944: II. Genetics 29.

HAWKES, I. G.: 1941: Potato collecting expeditions in Mexico and South America. Imp. Br. Plant Breed. a. Gen. II, 1944.

- FREISLEBEN, R. u. LEIN, A., 1944: Röntgeninduzierte Mutationen bei Gerste. *Züchter* 16.
- McFADDEN, E. S. u. SEARS, E. R., 1946: The origin of *Triticum Spelta*. *J. Heredity* 37.
- KIHARA, H., 1944: The synthesis of *Triticum Spelta*. *Agr. a. Hort.* 19. Tokyo.
- STUBBE, H. u. BANDLOW, G., 1947: Mutationsversuche an Kulturpflanzen. *Züchter* 17/18.
- LEIN, A., 1949: Asiatische Weizensortimente. *Kühn-Arch.* 62.
- BRÜCHER, H. u. ÅBERG, E., 1950: Die Primitivgersten des Hochlandes von Tibet. *Ann. Kgl. Landw. Hochsch. Schwed.* 17.
- SCHIEHMANN, E., 1951: Neue Gerstenformen aus Osttibet und ein weiterer Fund von *Hordeum agriocrithon*. *Ber. Dt. Bot. Ges.* 64.
- für Zea: 1945–1950 *Bot. Mus. Leaflets Harvard University* 10–14 1948 *Ann. Miss. Bot. Gard.* 35 IV.

#### B) prähistorisch:

- IVERSEN, J., 1941: Landnam i Danmarks Stenalder. *Danm. Geol. Unders.* II. R. Nr. 66.
- 1949: The Influence of prehistoric Man on Vegetation. *Danm. Geol. Unders.*, IV. R., Bd. 3. Nr. 6.
- JESSEN, K. u. H. HELBÆK, 1944: Cereals in Great Britain and Ireland in prehistoric and early historic times. *Kgl. Danske Vidensk. Selsk. Biol. Skr.* III/2.
- LIBBY, W. F., 1946: *Physical Review* 69.
- 1952: Radiocarbon dating. Un. Chicago Press.
- SCHARF, A. u. MOORTGAT, A., 1950: *Aegypten und Vorderasien im Altertum*. Brockmann, München.
- GROSS, H., 1952: *Die Radiocarbon-Methode. Eiszeitalter und Gegenwart* 2.

#### C) neuste Probleme:

- DEBONO, F., 1948: El Omari. *Ann. Serv. Ant. Egypte* 48.
- LAUER, J. P., TÄCKHOLM, V. L., ÅBERG, E., 1950: Les Plantes découvertes dans les souterrains de l'enceinte du Roi Zoser à Saqqarah. *Bull. Inst. Égypte* 32.
- HELBÆK, H., 1952: Spelt in Bronze Age in Denmark. *Acta Archaeologica* 23.
- 1953: Queen Ichetis' Wheat. *Kgl. Danske Vidensk. Selsk. Biol. Medd.* 21, Nr. 8.
- SCHIEHMANN, E., 1954: Einkorn im alten Aegypten? *Züchter* 24.
- MAC KEY, J., 1954: Neutron and X-ray experiments in Wheat and a revision of the speltoid problem. *Hereditas* 40.
- WERNECK, H. L., 1949: Ur- und Frühgeschichtliche Kultur- und Nutzpflanzen in den Ostalpen. *Schriftenreihe der O. Ö. Landesbaudirektion* No. 6.
- HOFMANN, E., 1953: in: *Der vollneolithische Roggenfund von Wien-Vösendorf* von H. Landenbaur-Orel. *Veröff. Histor. Museums Stadt Wien* H. 2.



## Antarctic Flowering Plants

By C. SKOTTSBERG

The first truly Antarctic flowering plant was discovered and collected by Dr. JAMES EIGHTS in the South Shetland Islands in the summer 1829–30. EIGHTS, “a pioneer Antarctic naturalist”, as W. T. CALMAN (*l*) calls him, accompanied an American sealing cruise as surgeon and biologist. From the introduction to his paper on a new Crustacean (1833) CALMAN quotes p. 177 “a small species of *Avena*”, adding that it probably was *Deschampsia antarctica* (HOOKER)—the word “probably” might have been omitted. “The plants obtained by EIGHTS are said to be in the State Herbarium at Albany” CALMAN says (p. 174); there is, as far as I have been able to find out, no institution with that name now, and my efforts to locate the collection have not been successful. This is of no importance because part of the material reached Kew and was described by W. J. HOOKER as *Aira antarctica* HOOK. in 1837. The type, illustrated l. c. Pl. 150, is mounted on a sheet with J. D. HOOKER’s specimen from the Falkland Is. and on the sheet he has written “Dr. EIGHTS”; the label says “No. 2. S. S. I.” (= South Shetland Is.), written, as Dr. W. B. TURRILL kindly told me in a letter, by EIGHTS or by BERKELEY. J. D. HOOKER has added “D. Berk. *Aira antarctica* HOOK. N. S. Shetland” (= New South S.). According to Dr. TURRILL “D. Berk.” (= Dedit BERKELEY) indicates that “the specimen was given to HOOKER by the Rev. BERKELEY who had correspondents in America.”

W. J. HOOKER probably knew that there already existed an *Aira antarctica* FORSTER Prodr. 1786 p. 41 from New Zealand, perhaps also that FORSTER is quoted in KROCKER’s Flora Silesiaca IV, Suppl. tab. 1 (1823), but as FORSTER’s plant had been transferred to *Avena* by ROEMER et SCHULTES in 1817 and to *Trisetum* by TRINIUS in 1831 he felt at liberty to use the name *antarctica* under *Aira*. DESVAUX (3, p. 338) removed it from *Aira* and placed it under *Deschampsia* where it remained as *D. antarctica* (HOOK.) DESV. until PARODI found that the specific epithet of

HOOKEr was illegitimate when coined and that the first legitimate name was *Airidium elegantulum* STEUDEL 1855 (15, p. 423) so that the correct combination had to be *Deschampsia elegantula* (STEUDEL) PARODI, 1949 (10, p. 452)—another wellknown name of a famous species, quoted in scores of books and papers, had to disappear. However, Dr. TURRILL pointed out to me that Art. 81 of the International Rules comes to our rescue: if we write *D. antarctica* DESV. leaving out (HOOK.) everything is in good order.

*D. antarctica* was rediscovered in the Antarctic by E. RACOVITZA in 1898 during the Belgian Antarctic Expedition, reported from a single station in the Gerlache Channel, and the only place where I saw it in 1902 is in the same region. I got the impression that it was very rare, but later surveys have shown that it is widely distributed, as seen from the list of localities below.

### *Deschampsia antarctica* DESV.

Icon.: W. J. HOOKEr (8, t. 150); J. D. HOOKEr (7, t. 133); MACLOSKE (9, p. 200, fig. 37 — very poor); SCHENCK (12, p. 23, fig. 6, and 13, p. 107); PARODI (10, p. 453, fig. 13).

South Shetland Is, EIGHTS' (K, type); King George I., Admiralty Bay, L. GAIN 26.12.1909 "en quantité", and on an islet in the west branch of the bay, GAIN 30.12.1909, "quelques touffes" (6, p. 100); I have not been able to find out where his collection is preserved; King George I., Admiralty Bay, 62°58's., a) A. G. BENNETT 13.11.1925, "up to 60 ft alt., frozen hard", and 27.11.1925 "in a dense tussocky formation near Penguin Rookery. This is used by gulls for nest making" (both B. M.); b) East side of Machellar (= Mackellar) Inlet, Discovery Exp. St. 1954, 21.1.1937 (B. M.) "in crevices of rocks at sea level. Grass tufts very meagre and small as collected"; c) Near Martin's Head, Discovery Exp. St. 1950, 7.1.1937 (B. M.) "a few feet above sea level, from small tufts and patches on slopes of volcanic tuff" and "100 feet above sea level small portions of large divot-cut from patch of close turf at least 50 square yards in area Soil underneath at least 8–10 inches deep"; d) B. FRÖDIN 5.1.1953 (S). — Deception I., Ronald Crater near Whalers' Bay near sea level in cinder plain, I. MACKENZIE LAMB n. 2322, 8.3.1945 (B. M.); "the only tuft seen".

South Orkney Is. On hillside facing N, alt. about 50 ft, T. HOOLEY n. 3029, Feb. 1944 (B. M.); Signy I., Discovery Exp. St. 1962, 13.2.1937 (B. M.) "growing fairly luxuriantly a few feet above sea level, a yard or two to the right of the old whaling station at Borgi (= Borge) Bay. In patches as much as a yard or two square."

Graham Land (Palmer Peninsula). Gerlache Strait, Danco Coast, Cape van Beneden, E. RACOVITZA 1898 (16, p. 8; the material seems to have been lost); Cape Rasmussen n. e. of Cape Tuxen (65°16's., 64°07'w.), L. GAIN March 1909 (6, p. 80); Cape Trois-Perez 11 miles s. of Cape Tuxen, GAIN l. c.

Palmer Archipelago. Brialmont Bay, Moss I., c. 64°05's., C. SKOTTSBERG

1902 (S). – Melchior Is., Lysted I., 64°19's., P. A. SIPLE n. 336, 1.3.1941 (US, BM, K, G, S); Sobral I., Cape Dos Monjes, A. T. HUNZIKER n. 10196, 6.2.1953 (S ex Herb. PARODI): “escasa en fissuras de rocas y pequeñas depresiones, formando matitas aisladas en altos acantileros costales”; Anvers I., Biscoe Bay near Cape Lancaster (64°51's., 63°42'w.), J. TURQUET n. 407–409, 10.2.1905 (2, p. 114), “sur massif de rochers en désagrégation (P, K); Wiencke I., Port Lockroy, 64°49's., 63°31'w., I. MACKENZIE LAMB n. 2147, 30.12.1944 (B. M.), “Near the penguin rookery, altit. circ. 15 feet, in narrow crack between almost vertical and horizontal granodiorite faces, north exposure”.

Argentine Is., Berthelot Islets 5 miles s. of Cape Tuxen (65°16's., 64°07'w.), GOURDON Jan. 1909 (6, p. 76).

Dannebrog Is., Petermann I., 65°11's., 64°10'w., GAIN 1.–10.1.1909 (6, p. 76). Biscoe Is., 65°30's., 66°w., F. BEHN 19.3.1952 ((Conc., S).

Adélaïde Is., Léonie I., GAIN 17.1.1909, and Jenny I., 15.1.1909, 67°45's., 68°50'w. (6, p. 76), only stations s. of the Polar Circle where flowering plants have been found.

**General distribution.** South America along the Andes from c. 34°n. (Curicó in Chile and Mendoza in Argentina) to the Fuegian Archipelago; Falkland Is., South Georgia, Prince Edward Is., Crozet Is., Kerguelen, Heard I., West Antarctica.

In the place where I observed *Deschampsia* in 1902 it formed scattered tufts in a closed moss carpet with northerly exposure, but the notes on some of the collectors' labels quoted above show that it occurs on different kinds of soil where the ground is free of snow during the short Antarctic summer and that there are numerous small areas on little islands lacking the usual ice cover where conditions for plant growth are favorable; on the mainland and larger islands such spots are very few except, perhaps, in the South Shetlands. On the east side of the Trinity-Louis-Philippe peninsula no phanerogams have been found (14).

Under special circumstances *Deschampsia* will form patches large enough to allow us to speak of a *Deschampsia* sociation, either more or less pure or with a bottom layer of bryophytes and lichens. It was observed with flowers everywhere. They are cleistogamous. The tufts are rarely over 5 cm. high, overtopped by the panicles which may reach a height of 10 cm. In the Subantarctic zone, as in the Falkland Is. or on South Georgia, Kerguelen, etc. it reaches greater dimensions; the blades may become 10–15 cm. long, the panicle 20–25 cm., but in exposed situations it gets stunted. The spread of the panicle is lesser in the Antarctic plant, but I have seen Subantarctic specimens very like Antarctic ones also in this respect. To the descriptions given by HOOKER, DESVAUX,

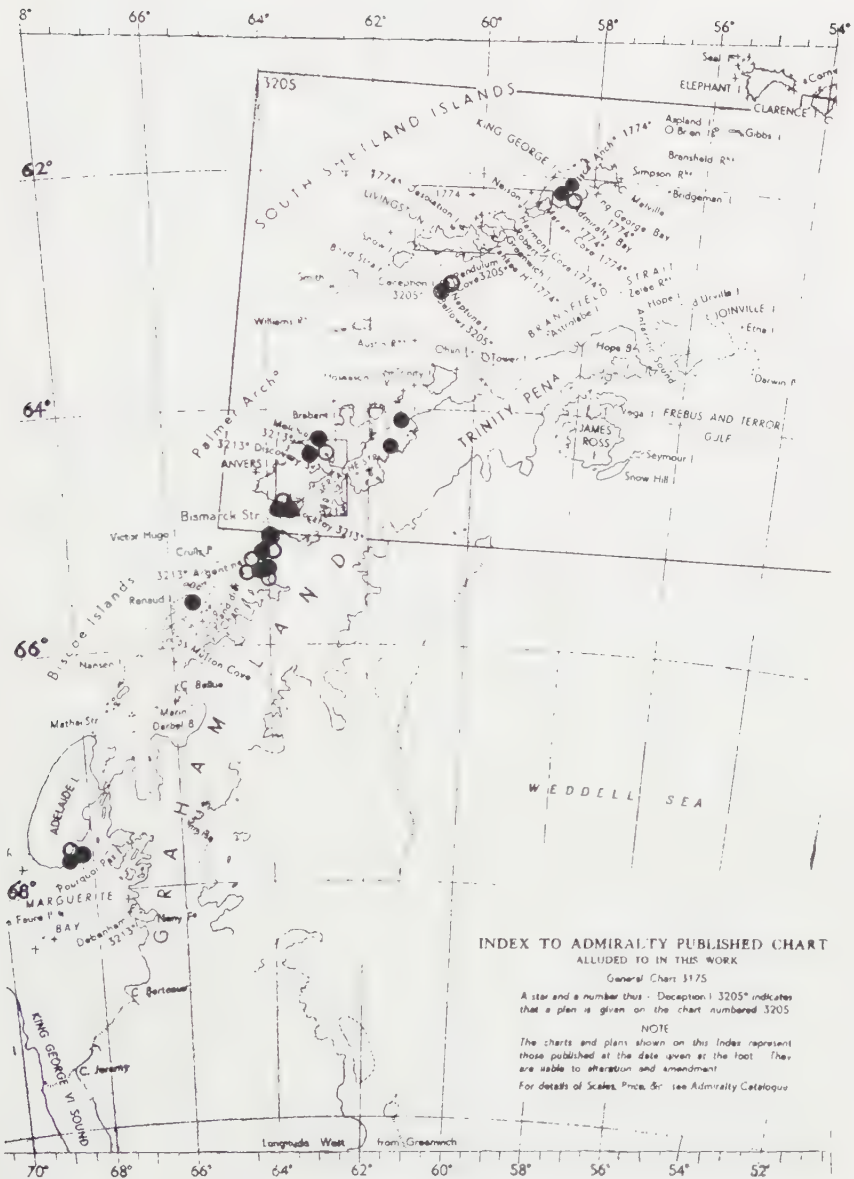


Fig. 1. Map of the Graham Land region (after The Antarctic Pilot) showing distribution of Phanerogams. The South Orkney Is. lie outside this map. *Deschampsia antarctica* (dots) - *Colobanthus crassifolius* (rings).

PARODI etc. may be added that the figure 0.5–1 mm. for the width of the blade applies to the convolute leaf; when unrolled it measures 2.5–3 mm.

During CHARCOT's first antarctic expedition *Colobanthus crassifolius* (*Caryophyllaceae*) was discovered in the far south by J. TURQUET. Later many new localities have been added, and even if *Colobanthus* is a rarer plant than *Deschampsia* it occupies the same area; see map, Fig. 1.

*Colobanthus crassifolius* (D'URV.) HOOK fil.

Icon.: D'URVILLE (4, Atlas, tab. 17, fig. E).

South Shetland Is., King George I., Admiralty Bay, 62°58's. a) An islet in the west branch of the bay, L. GAIN 30.12.1909 (6, p. 100), scarce; b) A. G. BENNETT 25.11.1925 (B. M.); c) East side of Machellar (= Mackellar) Inlet, Discovery Exp. St. 1954, 21.1.1937 (B. M.) "in crevices of rocks at sea level. Growing as very small cushion." A single small semiglobose cushion c. 1.5 cm. high. – Deception I., F. BEHN n. 12494, 5.2.1952 (Conc., S). Dense but not very hard cushions in fruit.

South Orkney Is., Signy I., Discovery Exp. St. 1962, 13.2.1937 (B. M.) "growing fairly luxuriantly a few feet above sea level, a yard or two to the right of the old whaling station at Borgi (= Borge) Bay. In patches as much as a yard or two square. Forms cushions as collected." Evidently scattered in the patches of *Deschampsia*, see under this. Small, semiglobose and very compact cushions, 5–6 cm. across and 3–4 cm high. Sterile.

Palmer Archipelago, Melchior Is., Lysted I., 64°19's., P. A. SIPLE n. 337, 1.3.1941 (US, S). Hard cushions in fruit, interwoven with mosses; Anvers I., Biscoe Bay near Cape Lancaster (64°51's., 63°42'w.), J. TURQUET n. 409, 11.2.1905 (2, p. 114, P).

Dannebrog Is., n.w. coast of Petermann I., 65°11's., 64°10'w., GAIN, March 1909 (6, p. 80).

Argentine Is., Galindez I., 65°15's., 64°16'w., Brit. Grah. Ld. Exp. n. 1388, 14.12.1935 (B. M.).

Graham Land, Cape Rasmussen n. e. of Cape Tuxen (65°16's., 64°07'w.), GAIN l. c.; Cape Trois-Perez 11 miles s. of Cape Tuxen, GAIN l. c.

Adélaïde Is., Jenny I., 67°45's. 68°42'w., GAIN l. c., p. 76, 15.1. and 30.1.1909. In flower.

General distribution. S. Chile, West Patagonian channel region, Fuegian Archipelago, Falkland Is., South Georgia, West Antarctica.

In his diary for Feb. 11, 1905 (Biscoe Bay), CHARCOT wrote (2, p. 114): "Mes camarades y trouvèrent une végétation abondante pour ces régions et rapportèrent même deux Phanérogames, inconnues jusqu'alors." Of these *Deschampsia* had long been known from the Antarctic. GAIN l. c., p. 78, referred *Colobanthus* to var. *brevifolius* ENGLER (5, p. 283) from South Georgia, leg. MOSTHAFF. I have examined a good set of this (S);



leaf blades 4 mm. long or even less, flowers as a rule not much raised above the surface of the cushion. I collected exactly the same form in South Georgia in 1902, but also other specimens with blades twice as long and pedicels well developed, and in one station the cushions were quite lax, the blades varied from 6 to 15 mm. in length and the flowers were well exposed above the cushion. According to ENGLER the total length of the leaves is 6–7 mm. in the variety which agrees with D'URVILLE's illustration of the type material, a very compact, short-leaved form. In any case, there seems to be no reason to segregate varieties based on leaf size.

It caused some sensation when the occurrence in the Antarctic of a third indigenous phanerogam was reported by PARODI (10, p. 457): *Deschampsia parvula* (HOOK. fil.) DESV., collected by TURQUET ("Turqueb") with *D. antarctica*; for "et des aggregations" read "en désagregation". I am obliged to the Director of the collection of flowering plants in the Mus. Nat. Hist. in Paris for the loan of TURQUET's entire material of *D. antarctica*, which I found to be quite uniform and to represent only this species. As PARODI does not quote TURQUET under *antarctica* (*elegantula*), he must have referred all his material to *parvula*, but the sheets bear no remark in his hand. In his paper he expressed as his opinion that *parvula* seems to be a "variación densiflora" of *elegantula*, differing only by the more compact tufts, by its smaller size and by the contracted, almost spike-like panicle, and in a letter to me, which was accompanied by a small sample of *D. parvula* from Basket I., Tierra del Fuego, SPEGAZZINI n. 20701, and by a specimen of *D. antarctica* from the Antarctic, HUNZIKER n. 10196, he expresses his belief that the two species ought to be united because no floral characters permit us to separate them. I regret that I cannot share the opinion of the eminent agrostologist. Even if the nature of the tuft and leaves is the same in both, the shape of the panicle is different and there are no transitions. Glumes and lemmas are much the same in both, the glumes varying in length between 5 and 7 mm. (mostly 5.5–6.5), the lemmas between 2.5 and 4 mm. (mostly about 3 mm.); anthers 0.4–0.5 mm. in *antarctica* 0.5–0.7 mm., in *parvula*. PARODI's figs. 13 and 15 give the impression that the spikelets of *parvula* are larger than those of *antarctica*, but his illustration of the latter represents the type of STEUDEL's *Airidium*, LECHLER n. 1220 from Punta Arenas. According to STEUDEL the glumes measured only  $1\frac{1}{2}$  lines (3 mm.), but they are 4.6 mm. long on PARODI's figure, an unusually small size for this species. In another specimen from

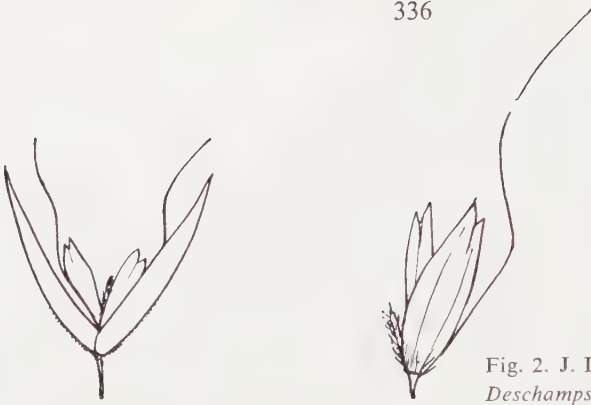


Fig. 2. J. D. HOOKER's drawing of *Deschampsia parvula* (type K).  $\times 4.7$

Punta Arenas (S), labelled *Airidium elegantulum*, they are 4.7–5.3 mm. long.

There is, however, another character which seems to hold good and to distinguish *parvula* from *antarctica*, the geniculate arista, a character not mentioned by PARODI, but clearly expressed in his figure 15 B (SPAGAZZINI n. 20702 from Gregory Bay, Tierra del Fuego) and mentioned in HOOKER's diagnose (7, p. 377) as also by DESVAUX (3, p. 339): "arista geniculata" against "arista recta" in *antarctica*. On my request Dr. E. ASPLUND looked up the type of *D. parvula* (K) and reported (see also PARODI, l. c., p. 455), that all the spikelets except one had lost their florets and that the single remaining one could not be analysed, but that the specimen is accompanied by a sketch which Dr. ASPLUND copied. It is reproduced above, Fig. 2. I have collected *D. parvula* in the mountains back of Ushuaia 530 m. s. m. (n. 221, S) and in the Falkland Is., New I. (n. 130, S). These specimens agree with the type.

The differences in the morphology of the arista do not end here. PARODI remarks that, in *parvula*, the lower portion is spirally twisted, but not so in *antarctica*; I can only confirm the correctness of this statement. Moreover, when PARODI calls the awn "débile" in *antarctica*, he hints at another character which seems to be constant. I have examined specimens from Patagonia, Tierra del Fuego, the Falkland Is., South Georgia and the Antarctic. The diameter, not counting the long tapering apical portion, varies between 0.02 and 0.038 mm. as extremes and as a rule between 0.022 and 0.03 mm., whereas in *parvula* from Tierra del Fuego and the Falkland Is. the figures are 0.042 to 0.055, in one case up to 0.06 mm. I think we have better retain *parvula* as a separate species, not found in the Antarctic.

The two Antarctic flowering plants are confined to the Graham Land region, where we find a fairly rich flora of Bryophytes (mainly mosses,

Hepatics being very few) and Lichens, among which a great number of species are considered to be endemic. Even if their number is likely to be reduced when the cryptogamic flora of Subantarctic America becomes better known, and the lichens in particular have been subject to a critical revision, a considerable endemic group will remain which is supposed to have survived since preglacial times. It has been shown that the ice-cover once had a much greater extension than now, and even if our knowledge of the details is insufficient, there can be little doubt that only scattered nunataks and more or less perpendicular rock faces offered suitable stations where plant life could exist, and this seems to be true also of the northernmost chain of islands. *Colobanthus* is an old Antarctic genus and *Deschampsia* well represented in the South, we have reason to believe that *C. crassifolius* and *D. antarctica* belonged to the Preglacial Antarctic flora, but we have no right to assume that they were able to survive the Glacial Epoch. It seems safer to regard them as Postglacial immigrants, the only Vascular Plants that managed to cross the wide Drake Strait and establish themselves successfully in high southern latitudes.

*Poa annua* L.

Deception I., Whalers' Bay, B. FRÖDIN 7.1.1953. A single, a few cm. high specimen (the only one observed), c. 5 m. above high water. In flower.—As far as I know this is the first record for a weed in the Antarctic.

### Bibliography.

1. CALMAN, W. T., 1937: James Eights, a pioneer Antarctic naturalist. *Proceed. Linn. Soc.* 149.
2. CHARCOT, J.-B., 1908: Expédition antarctique française (1903–1905). *Journal de l'Expédition*. Paris.
3. DESVAUX, E., 1853: Gramíneas in GAY, *Historia física y política de Chile*. Bot. 4.
4. DUMONT D'URVILLE, J., 1852: *Voyage au Pole Sud et dans l'Océanie*. Atlas, Dicot. Paris.
5. ENGLER, A., 1886: Die Phanerogamenflora von Südgeorgien. *Botan. Jahrb.* 7.
6. GAIN, L., 1910: Rapport sur les travaux de zoologie et de botanique. CHARCOT, *Rapports préliminaires sur les travaux exécutés dans l'Antarctique ... de 1908 à 1910*. Institut de France, Paris.
7. HOOKER, J. D., 1844–47: *The Botany of the Antarctic Voyage*. I. Flora Antarctica. London.
8. HOOKER, W. J., 1837: *Icones Plantarum* 2. 1837.

9. MACLOSIE, G., 1908: Flora Patagonica. Rep. Princeton Univ. Exped. to Patagonia 1896-99. *VIII*.
10. PARODI, LORENZO R., 1949: Las Gramíneas Sudamericanas del Género *Deschampsia*. *Darwiniana* 8.
11. The Antarctic Pilot. 1948: Second edition. London.
12. SCHENCK, H., 1905: Vergleichende Darstellung der Pflanzengeographie der subantarktischen Inseln. *Wiss. Ergebn. Tiefsee-Exped. Valdivia* 2.
13. — 1928: Die Gefäßpflanzen. *Deutsche Südpolar-Exped. 1901-03. 8. Botanik*.
14. SKOTTSBERG, C., 1912: Einige Bemerkungen über die Vegetationsverhältnisse des Graham-Landes. *Wiss. Ergebn. Schwed. Südpolar-Exped. 1901-1903. 4. Botanik*.
15. STEUDEL, E. G., 1855: *Synopsis Plantarum Glumacearum I*. Stuttgart.
16. WILDEMAN, E. DE, 1905: Les Phanérogames des Terres Magellaniques. *Rés. Voyage S. Y. Belgica. Rapports scientifiques*. Anvers.

# Adaptation of Small Plants to Deficient Nutrition and a Short Growing Season

Illustrated by Cultivation Experiments with *Capsella  
bursa pastoris* (L.) MED.

By THORVALD SØRENSEN

## 1. Introduction.

Small plants chiefly occur in localities in which the nutritive conditions are unfavourable or where, for some reason or other, the growing season is abnormally short. This directly observable fact is probably generally regarded as a simple expression of the slight yielding power of the soil in the particular localities. The vegetation of the grey dune is an example of a community of small plants growing in soil which is extremely poor in nutritive substances. Old gravel pits are colonised by the least exacting weeds of the surrounding area, which are here often able to fructify in spite of inconsiderable vegetative development. As an example of localities which offer only a short growing period to the plants, dry slopes exposed to the sun, where the water supply fails in the early summer, may be mentioned. Small winter annuals such as *Cerastium semidecandrum* and *Erophila verna* seem to find optimal conditions here. Further, late-drying flat lake-shores with *Juncus bufonius* and its companions of dwarfs. Where scarcity of nutrition and reduction of the growing season exert their influence at the same time, our smallest plants such as *Radiola*, *Centunculus*, and *Juncus pygmaeus* will assemble.

*A priori* there is hardly any reason to assume that the plants should react in the same way to scarcity of nutrition and shortness of time. Even though the result is evidently the same, namely small plants, logically we are concerned with two entirely independent manifestations: In one case a result of the economising of the plant, in the other case a *fait accompli*. In other words, in one case we are confronted by the mani-



festation of a modified phenotype as a common exponent of the genotype and poor life conditions (pheno-dwarfs), in the other case by the direct exponent of the genotype (geno-dwarfs).

On immediate consideration it seems evident that the small plant will be capable of completing its development in a shorter time than the big one. However, the problem is hardly so simple. The question is what relation exists between the size and the phasic development. This question cannot be directly answered, for it resolves itself into two: What constructional properties are associated with 1) a small absolute size, and 2) a rapid development (early flowering)? These questions might probably be much more fully elucidated than seems to have been done so far, by simple analysis of herbarium material. However, the problem of the dwarf plants has also other aspects, which can only be elucidated by experiments. The question then arises: To what extent will deficient nutrition affect 1) the constructional character of the plant, 2) its growth rate, and 3) its phasic development?

The problem of the small plants, as tentatively outlined above, concerns such simple phenomena as the absolute dimensions of the plants, their number of leaves, and their flowering time. These aspects of the ecology of the plants deserve, no doubt, more attention than has hitherto been given to them. The small and ephemeral plants form such extremes as we need in order get a keener eye for problems of more general scope. An experimental treatment of the above-mentioned questions can probably be most easily done by means of annual plants. Therefore, for my experiments I have preferably chosen such plants for cultivation partly under favourable, partly under extremely unfavourable conditions of nutrition. The present paper deals only with a single series of cultures, carried out in 1950 with different biotypes belonging to one and the same Linnean species, *Capsella bursa pastoris*.

## 2. Method and material.

The experiment was carried out as follows:

The seed samples were sown in flower-pots in a frame (April 18th). When the seedlings had developed two leaves in addition to the cotyledons, ten plants of each sample were planted out in open ground in ordinary garden soil and ten in flower-pots with coarse sand, five in each (May 5th). The dimensions of the flower-pots (internal measures) were: diameter at the top 12 cm, at the bottom 7 cm, height 10.5 cm; area accordingly 114.5 cm<sup>2</sup>, volume 732 cm<sup>3</sup>. The pots with sand cultures were

at once placed in the open and were watered with tap-water all during the summer. Care was, of course, taken that the roots should not grow out through the bottoms of the pots.

The development of rosette leaves (number of leaves) was registered for each plant at intervals of about ten days, certain numbered leaves being marked with white oil-paint. Such a continual registration of the increment of leaves is necessary for an ascertainment of the final number of leaves, as the lowermost leaves gradually wither and fall off. A determination of the number of leaves of full-grown plants on the basis of the leaf-scars cannot be made with even an approximate accuracy. In the course of the early summer a number of the plants were dissected in order to ascertain the formation of flower buds. The final number of leaves can then be determined even while the flower buds are young and concealed in the leaf rosette. As the time-consuming marking of the leaves had to be given up in July, only a minimum limit for the number of leaves can be given for a few late-flowering strains. In addition to the development of leaves, the incipient flowering was registered for the earliest and the latest plant (of the remaining ones) within each set. At the end of the experiment representative plants of all the samples of the garden soil series and a number of the samples of the sand series were dried for later weighing.

For further orientation the following observations may serve: The siliques ripen ca. 3 weeks after flowering. In the garden soil plants the flowering (even on the main axis) extends over a longer period, so the very same inflorescence may have shed the seed of the lowermost siliques while fresh flowers are still developed at the top. At the same time lateral shoots appear in the axils of stem leaves, in a few types, however, principally in the axils of rosette leaves. These secondary axes often continue flowering longer than the main axis. The sand culture plants generally remain unbranched, and the flowering of the main axis is often completed early; the siliques of these plants, therefore, ripen almost simultaneously.

The seed samples used were in most cases not derived from single plants, but from populations. This possibly contributed to the great variation in the flowering time of some of the samples, which must probably be ascribed to a genetic dissimilarity. The variation caused some trouble in the assessment of the correlation between the number of leaves and the flowering time (cf. p. 346). It should be noted, however, that each strain, in spite of variation in flowering time, as a rule exhibited a certain degree of uniformity, in leaf form as well as in type of branching and shape of the siliques. As already pointed out by ALMQUIST (1907,

1921), *Capsella bursa pastoris* includes a large number of local races. ALMQUIST describes no less than ca. 200 "species". No "specific" determination of my experimental material was attempted, nor would such a determination probably be of any great interest for the problem considered here.

The experimental material comprises a number of samples from Denmark and southern Sweden as well as a single sample from Greenland. A list of the provenance of the samples is given below. To facilitate the understanding of the experimental results dealt with in the subjoined sections, the samples were re-numbered and listed in succession according to incipient flowering in the garden soil series (cf. fig. 2).

1. Copenhagen, the garden of the Royal Agricultural College, Rolighedsvej. Garden paths.
2. As no. 1.
3. Copenhagen, garden of the Royal Agricultural College, Rolighedsvej. Garden beds.
4. Greenland, Ivigtut, waste place.
5. Sealand, north side of Haraldsted Lake. Dry south-facing slope.
6. Sealand, east of the lake Skarritsø. Dry road slope.
7. Sealand, Vellerup. Dry dike across luxuriant cultivated field.
8. Sealand, Sonnerup near Holbæk. Waste place of recent date.
9. Västergötland, Vårgårde. Moist cultivated field on peaty soil.
10. Sealand, Lynge-Bastrup. Roadside of newly laid out road.
11. Sealand, Reersø. Along the shore, above washed-up seaweed.
12. Sealand, near the town of Roskilde. Rubbish with luxuriant (nitrophilous) vegetation.
13. Öland (Sweden), near Dalby Forest. Dry meadow near the Alvar.
14. Sealand, Vridsløselille railway station. Gravel-covered platform.
15. Öland (Sweden), Smedby. Place near summer house.
16. Öland (Sweden), Ottenby. Shore cliff near stream of surface water.
17. Västergötland, Vartofte, near pool of water, nitrophilous vegetation.
18. Sealand, near Vridsløselille. Cultivated field, luxuriant, clayey mull.
19. Sealand, Haraldsted. Old fruit plantation.
20. Öland (Sweden), Dalby. Near stone fence at the Alvar.
21. Sealand, near Vridsløselille. Cultivated field, luxuriant, clayey soil.
22. Rømø. Uppermost zone of littoral meadow, between the *Puccinellia* zone and the dike. Moist sandy soil.

### 3. Rate of increment measured by the number of developed leaves.

As the basis for an estimation of the growth rate of garden soil and sand plants I used counts of leaves registered on (May 5th), May 23rd, June 2nd, and June 22nd, as well as counts of the leaves of dissected

Table 1. Leaf development 5.V-22.VI. Average for the series.

	5 May		23 May		2 June		22 June			
	Leaves fully developed	Increase (variation)	Leaves fully developed	Increase (variation)	Leaves fully developed	Increase (variation)	Leaves fully developed	Leaves partly developed, green	Leaf primordia, pale	Leaves + primordia, total
Garden soil series .	2	6 (4-7)	8	6 (5-9)	14	24 (20-30)	38	13 (11-16)	30 (29-33)	81
Sand series . . . . .	2	4 (3-5)	6	4 (3-5)	10	12 (10-15)	22	8 (6-10)	19 (15-25)	49

plants largely carried out about the date of the last registration. The majority of the strains behaved almost alike, so the results can be given summarily in the form of tables (table 1). Particularly deviating strains are mentioned below.

The number of  $\pm$  fully developed leaves found is indicated for the dates of reading, beginning with the date for planting-out, May 5th. For June 22nd the number of partially developed green leaves and the number of  $\pm$  pale leaf primordia are registered, observable right to the growing point by dissection of the plant. It should be mentioned here that the number of partially developed green leaves have only reference to plants not yet stocking, and that the number of pale leaf primordia has only reference to plants which have not yet an observable floral axis. Thus the first readings comprise all the strains. The reading on June 22nd of fully and partially developed leaves still comprises about half the number of strains, while the number of pale primordia as regards the garden soil series has only reference to three samples (nos. 19, 21, 22); as to the sand series, however, to ten samples. The numerical values mentioned are the means (of the individual sets) rounded to the nearest integer. The range of variation (mean of sets) is added in parenthesis.

It appears from table 1 that the leaf development in both series takes place at a constantly increasing rate, but that the starved plants in the course of the growing period become increasingly retarded as compared with the normally nourished plants. In the course of the twenty days from June 2nd to 22nd the starved plants were able to produce only half the number of leaves produced by the normally nourished plants.

A fact which does not appear from the table indicating the mean values for all the strains, is that the relation between the number of leaves of the garden soil plants and that of the sand plants was in most cases the

Table 2. Leaf development 5.V–22.VI of three extreme biotypes, compared with the mean (cf. table 1).

		5 May	23 May	2 June	22 June
No. 9.....	garden soil	2	8	17	(52)
	sand	2	6	11	(35)
No. 22.....	garden soil	2	6	10	27
	sand	2	6	9	19
No. 20.....	garden soil	2	7	12	35
	sand	2	6	9	27
Mean of all strains	garden soil	2	8	14	38
(cf. tab. 1)	sand	2	6	10	22

same. That is to say that the same strain will always be at the head of, respectively the bottom of, the two series of nutrition. Thus, in table 2 the numerical values for the leaf development of the fastest (no. 9) and the slowest (no. 22) growth type (mean for the sets) are compared. The rapidly growing sample no. 9, Västergötland, moist cultivated field, morphologically represents a special type distinguished by its large number of stem-leaves (ca. 10, in the other strains varying from 1–2 to 7–8) and an exceptionally abundant development of lateral axes from the rosette (in the garden soil plants; the sand plants produce no lateral axes). At the reading on June 22nd this strain was in incipient flowering, so the number of leaves for this date is hardly directly comparable with table 1. The slow-growing no. 22 is a shore form from Romo. The plant has a low bushy growth. The same growth type is found in no. 16, shore cliff, Öland, but here it is not combined with a particularly slow development of leaves. It should be mentioned that the rapid, respectively slow, production of leaves in these two extreme strains is revealed to the same extent by both nutrition series.

Deviating reaction to the nutritive conditions is shown by nos. 13 and 20, both from the Alvar area of Öland. It is immediately obvious from table 2 that no. 20 shows a relatively slight difference in the rate of leaf development for the two nutrition series. These strains are apparently less retarded by poor nutrition than the others. It is noteworthy that the garden soil plants were exceptionally small, small-leaved, and low-growing (cf. also table 3).



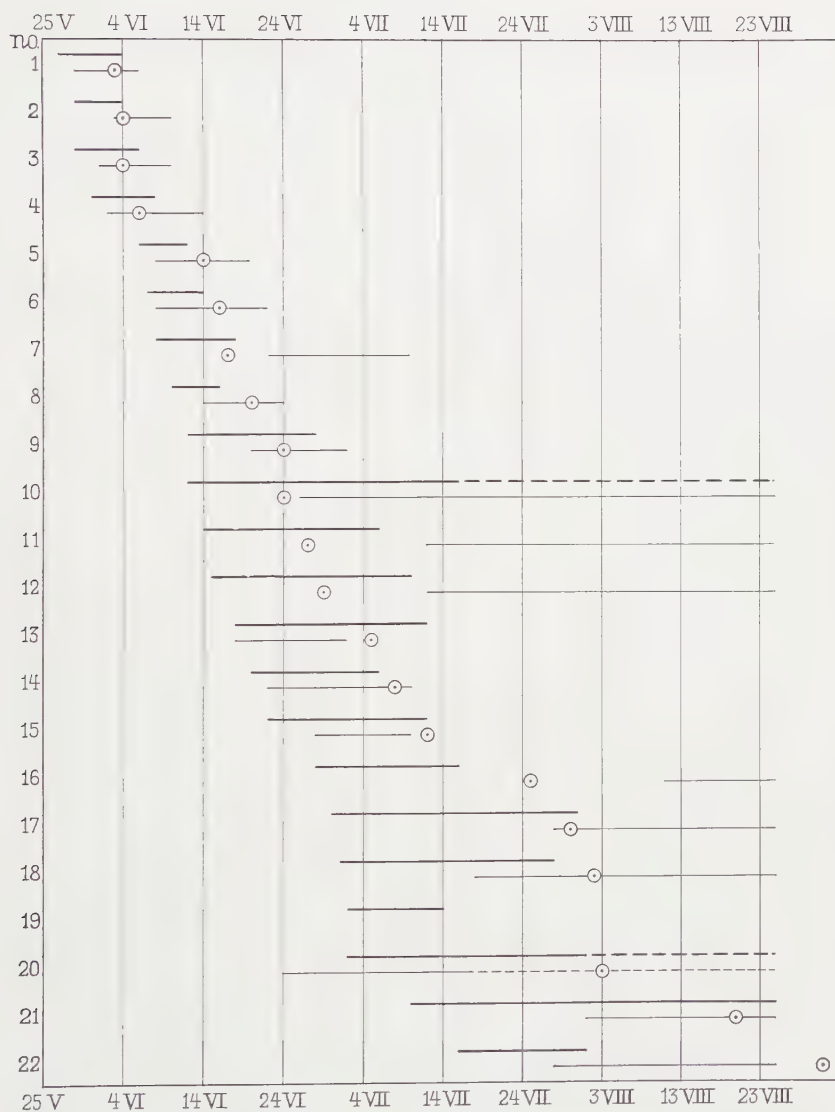


Fig. 1. Incipient flowering. Heavy line: the garden soil set. Fine line: the sand set. The length of the lines indicate the time interval between the incipient flowering of the earliest- and the latest-flowering plant. "Bird's eye" (⊙): see the text.

#### 4. Flowering time.

The flowering times for the different strains under garden culture and sand culture in pots are illustrated by fig. 1. The garden soil culture is indicated by the heavy line, the sand culture by the thin line. The starting

points of the lines indicate incipient flowering in the earliest plant of the set, while the end points indicate incipient flowering in the latest plant. A line interrupted to the right illustrates that only one single or a few late-comers are not yet in flower. The lines are not continued beyond 25.VIII. Plants which were not yet in flower on that day either had died already, or they died later in the autumn or the succeeding winter without flowering. Only a single plant, a sand culture plant (no. 21), survived during the winter and fructified next summer.

As was to be expected for a plant of such a simple structure as *Capsella*, there is a fairly close correlation between the number of leaves on the main axis and the flowering time: the smaller the number of leaves, the earlier the flowering. A graphical representation of the relation between the number of leaves and the flowering time is attempted in fig. 2. The representation is rendered difficult by the often varying flowering within the individual sets. To obtain the most suitable basis for a comparison of the strains, it was decided to figure the first incipient flowering (cf. fig. 1) in relation to the number of leaves. However, the available material of facts is not fully sufficient. For while the number of leaves is often determined by dissection of not fully developed plants in the flower-bud stage, the flowering time has reference to the remaining plants. However, the greatest possible care was taken to spare plants in various, also more advanced, stages. For want of a precise number of leaves for the first-flowering plant, the lowest leaf-number found for the set (ordinate) coordinated with the first flowering observed (abscissa) was used in the presentation in fig. 2. For a few very late-flowering strains the final number of leaves cannot be given, as the marking of the leaves was stopped too early during the experiment; in such cases the number of leaves found (including the leaf primordia) of the vegetative plant is indicated in the figure by an arrow (†) on the ordinate for incipient flowering.

In spite of the insufficiency of the material I consider it justifiable to represent the coordination between the number of leaves and the flowering time in the form of curves (fig. 2). Apart from certain irregularities in the position of the coordinate points (e. g. no. 14), which may thus be due to lack of real connection between the coordinated values, fig. 2 seems to give a fairly reliable picture of the actual conditions. The most remarkable irregularities are due to a deviating rate of growth for some few of the strains, as demonstrated above (e. g. no. 9: rapid growth in both series of nutrition; no. 20: relatively slow growth in garden soil, relatively rapid growth in sand). The differing courses of the curves for

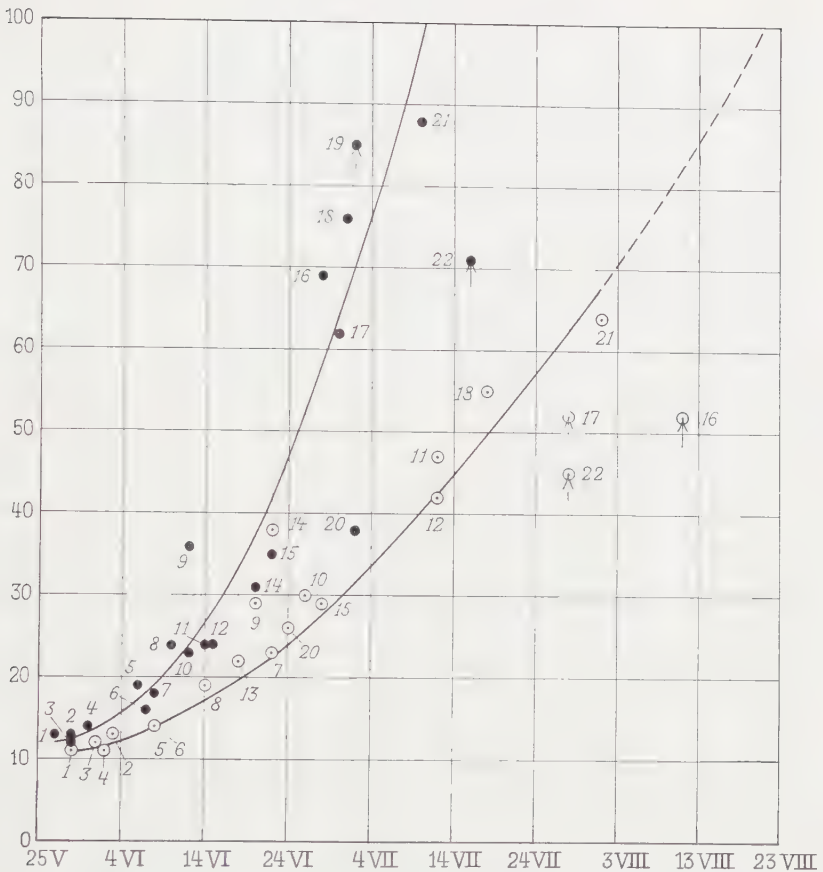


Fig. 2. Graphical representation of correlation between number of leaves and flowering time. Ordinate: number of leaves. Abscissa: time scale. Upper curve (●): garden soil series. Lower curve (○): sand series.

the garden soil series and the sand series, respectively, are indicative of the general difference in the growth rates of the two series. The chief purpose of fig. 2, however, is to illustrate the influence of the nutritive conditions on the structural character of the plants, *in casu* on their total number of leaves.

It is obvious that with the retarded development of the leaves which is characteristic of the sand plants, their possibility for flowering "in time" will depend on the degree to which the construction of a plant can be altered towards a reduction of the number of leaves. It is evident from fig. 2 that if the number of leaves is not reduced, the flowering of sand culture plants will be retarded by a period of time illustrated by the

horizontal distance between the two curves. The theoretical date thus determined for incipient flowering is inserted in fig. 1 (— $\odot$ —).

It will be seen from fig. 1 that the various strains show highly different behaviours. In most strains the sand plants reduce their number of leaves and thus attain a comparatively early flowering, e. g. nos. 6, 13, 14, 15, 20, and 22. Others, however, show an entirely reverse reaction; the number of leaves is increased, on which account the flowering will be further retarded or even fail, e. g. nos. 7, 11, 12, and 16.

The earliest flowering strains show a slight tendency to reduction of the number of leaves. Otherwise there is no recognisable connection between the flowering time and the mode of reaction.

### 5. Increase of weight during development, and total weight.

In tables 3a, 3b, and 4 the results of weighings of plants at different stages of development are given. The plants to be weighed were pulled up very cautiously in order that the main root and the strongest lateral roots should be preserved, and afterwards air-dried. The weighings were then carried out during the winter under laboratory conditions.

The tables give the date of collection and the number of plants; if several plants were weighed, only the mean weight is stated. Further, the developmental phase of the plants is recorded as follows:

- I. Plant entirely vegetative; main axis (growing point) not yet floral.
- II. Plants whose main axis (growing point) was recognisably floral, with flower buds, but not yet in flower.
- III. Plants with flowering main axis, the lowermost siliques not yet mature.
- IV. Plants with still flowering main axis (and possibly lateral axes), lowermost siliques mature.
- V. Flowering ceased, siliques mature; in the garden soil plants the seed on the lower part of the main axis had been shed.
- VI. All siliques mature; an essential part of the seed shed.

Tables 3a and b comprise weighings of the earliest flowering strains; table 4 weighings of the later flowering strains.

Table 3a shows that the weight of the garden soil plants had risen by five times in the period June 8th–20th, while the sand plants had not risen very much in weight. The garden soil plants continued flowering on the main axis for a long period and developed flowering lateral branches. The sand plants, however, remained unbranched; notably the plants of the early-flowering strains ceased flowering very early, so only few siliques

Table 3a. Total weight of experimental plants (nos. 1-6).

No.	8 June						20-22 June					
	Garden soil			Sand			Garden soil			Sand		
	Weight, g	Number	Phase	Weight, g	Number	Phase	Weight, g	Number	Phase	Weight, g	Number	Phase
1	0.81	2	IV	0.11	2	IV	4.77	1	V	0.05	2	V
2	0.94	2	IV	0.03	2	(III-)IV	4.78	1	V	0.04	4	V
3	0.90	2	IV	0.05	2	(III-)IV	2.72	1	IV	0.06	4	(IV-)V
4	0.65	2	IV	0.06	3	III-IV	3.30	1	IV	0.10	7	(IV-)V
5	0.90	2	III	0.08	2	III	5.27	1	IV	0.14	2	IV(-V)
6	0.61	2	III	0.02	3	III	5.33	1	IV	0.03	3	(III-)IV

Table 3b. Total weight of experimental plants (nos. 1-6) continued.

No.	3 July			5 July			1-2 August		
	Garden soil			Sand			Garden soil		
	Weight, g	Number	Phase	Weight, g	Number	Phase	Weight, g	Number	Phase
1	5.48	2	V	.	.	.	.	.	.
2	6.48	2	V-VI	.	.	.	.	.	.
3	.	.	.	.	.	.	.	.	.
4	10.46	1	V	.	.	.	.	.	.
5	17.42	1	V	0.07	4	V	19.42	1	VI
6	.	.	.	0.06	3	V	16.85	2	VI

were found. It will appear from both tables 3 and 4 that the final weight of the sand plants often amounted to only 1/100 or an even less fragment of that of the normally nourished garden soil plants.

A comparison of all the weighings from June 20th-22nd shows noteworthy correlations between the weight and the stage of development. Thus as for the garden soil plants it is quite evident that the weight increases with advancing phasic development or, in other words, the early-flowering strains attain the greatest total weight. Thus nos. 1-9, that is to say, plants at developmental stages (III-)IV-V, show a mean weight of 4.5 g, while the rest, nos. 10-22, chiefly at stages I-II, show a mean weight of 2.1 g. As regards the sand series, conditions are reversed, though less accentuated. If the same line of division is employed as was used above, the early strains (nos. 1-9) exhibit a mean weight of 0.08 g, the rest (nos. 10-22), the late-flowering plants, 0.12 g.

Even though the numerical material is rather limited, and the variation



Table 4. Total weight of experimental plants (nos. 7-22).

No.	20-22 June						1-2 August			Date: see foot-notes		
	Garden soil			Sand			Garden soil			Sand		
	Weight, g	Number	Phase	Weight, g	Number	Phase	Weight, g	Number	Phase	Weight, g	Number	Phase
7	3.42	2	IV	0.08	3	III	9.04	2	VI	.	.	.
8	4.80	2	IV	0.08	4	(III-IV)	13.48	2	VI	.	.	.
9	5.90	3	III(-IV)	0.12	4	III	39.32	2	V	.	.	.
10	2.27	3	II(-IV)	0.14	2	II	13.21	1	V	0.09	3	II-V <sup>3)</sup>
11	2.83	3	II(-IV)	0.08	2	I	15.78	2	V	0.24	2	V <sup>1)</sup>
	.	.	.	.	.	.	.	.	.	0.10	1	IV <sup>3)</sup>
12	2.77	3	II(-IV)	0.19	3	I-II	20.60	3	V	0.06	1	V <sup>3)</sup>
13	.	.	.	0.11	1	III	2.60	3	V	.	.	.
14	2.69	3	II(-III)	0.12	4	II(-III)	5.92	2	VI	.	.	.
15	2.21	1	III	0.06	3	II	21.38	2	V	.	.	.
16	2.16	2	II	0.07	2	I	14.48	2	V	0.09	3	I-II <sup>3)</sup>
17	1.92	2	II	0.13	1	I	10.44	3	(III-)V	0.07	2	IV-V <sup>1)</sup>
18	3.52	2	I-II	0.19	2	I	24.64	2	V	0.10	2	III-IV <sup>3)</sup>
19	1.00	1	I	.	.	.	6.40	2	V	.	.	.
20	0.44	2	II	0.04	2	II-III	3.23	1	V	.	.	.
	.	.	.	.	.	.	1.33	1	V <sup>2)</sup>	.	.	.
21	3.13	2	I	0.26	2	I	23.68	1	V <sup>2)</sup>	0.51	1	III <sup>1)</sup>
	.	.	.	.	.	.	.	.	.	0.57	1	V <sup>3)</sup>
	.	.	.	.	.	.	18.78	1	V <sup>3)</sup>	0.25	1	V <sup>4)</sup>
22	0.61	1	I	0.07	2	I	7.06	1	IV <sup>2)</sup>	0.20	4	IV-V <sup>3)</sup>

<sup>1)</sup> 1-2 August; <sup>2)</sup> 15 August; <sup>3)</sup> 25 August; <sup>4)</sup> 12 October.

great, there can hardly be any doubt that the available results have revealed a nutrition-physiological problem which deserves discussion at some length. First, the sand plants: The relatively low weight of the early-flowering plants is probably connected with the fact that already when the flowering begins, the assimilation apparatus has reached its highest capacity, while on the other hand the continued development of rosette leaves in the late-flowering plants will contribute to a constant increase of the assimilation apparatus of these plants. As to the garden soil plants, the lead taken by the early-flowering plants might seem difficult to explain. After the flowering has begun, these plants, it is true, branch profusely, but the secondary axes bear no or, in the best case, only a few and quite small leaves. Thus the branching does not at first sight result in any very great increase of the assimilation apparatus. In this connection attention should be called to the possible importance of the

immature siliques as organs in the service of assimilation. The flat (compressed) siliques attain their final size astonishingly soon after flowering, in the course of a very few days. During the later part of the flowering, which goes on for a long time under constant growth of the rhachis of the inflorescence, the whole visible "foliage" of the plant consists exclusively of green siliques. If it is not assumed that the siliques are in an essential degree assimilatorily self-supplying, the enormous and protracted fructification would be quite ununderstandable. The correctness of the hypothesis seems at any rate to be strongly supported by the aforementioned results of weighing.

From the final weights for the late-flowering strains (table 4) it appears that the final yield varies greatly within the two nutrition series. In the late summer a number of the plants suffered from attacks by the white rust of the *Cruciferae* (*Cystopus candidus* LÉV.), which may have contributed to the variation: however, no highly attacked plants were used for weighing. Thus there seems to be every probability that the great differences in weight are mainly due to genetic causes.

The few weighings of sand plants belonging to the late-flowering strains testify to the poor output of their long growing period, but hardly give an adequate picture of the miserable conditions. Many plants gradually died the death of starvation in the rosette stage. Accordingly the weighed specimens comprise the most vigorous individuals, sometimes the only survivors. In connection with table 4 it should further be pointed out as to the garden soil series that the rapidly growing no. 9 attained a much higher final weight than any of the rest, while the slow-growing no. 22 only showed a rather poor result. Further, the low weight of the two strains from the Alvar area of Öland, nos. 13 and 20, should be noted.

## 6. Seed production.

The success of the annual plant can probably best be measured by its seed production, its "reproductive capacity" (SALISBURY, 1942). The final values listed in tables 3-4 are expressions of their production of matter, but not of their effective productivity, their seed production. A weighing of the total seed production is not feasible in practice for the garden soil plants, which have already shed part of the seed before the flowering is finally completed. Still, an approximate determination of the seed production is possible. The number of siliques can always be accurately determined, for if the seed and valves have been shed, the silique dis-

Table 5. Total weight of mature plants, number of siliques and quotient number of siliques/total weight (g).

No.	Garden soil				Sand				Siliques/g, mean	
	Date	Weight, g	Siliques	Siliques/g	Date	Weight, g	Siliques	Siliques/g	Garden soil	Sand
1	3.VII.	6.12	763	124	22.VI.	0.08	19	237	.	.
	—	4.83	736	152	—	0.03	9	300	138	269
2	3.VII.	8.27	1240	150	22.VI.	0.06	14	233	.	.
	—	5.40	839	156	—	0.04	11	275	..	.
	.	.	.	.	—	0.04	12	300	.	.
	.	.	.	.	—	0.03	8	267	153	269
3	.	.	.	.	22.VI.	0.03	8	267	.	.
	.	.	.	.	—	0.06	13	217	.	.
	.	.	.	.	—	0.06	13	217	.	.
	.	.	.	.	—	0.07	17	243	.	236
4	3.VII.	7.92	1373	173	22.VI.	0.05	14	280	.	.
	—	12.99	1780	137	—	0.11	23	208	.	.
	.	.	.	.	—	0.10	19	190	.	.
	.	.	.	.	—	0.06	16	266	.	.
	.	.	.	.	—	0.11	22	200	155	229
5	3.VII.	19.82	3456	174	22.VI.	0.02	5	250	.	.
	.	.	.	.	—	0.08	15	187	.	.
	.	.	.	.	—	0.07	13	186	.	.
	.	.	.	.	—	0.10	17	170	174	198
6	3.VII.	17.43	3077	176	5.VII.	0.03	4	133	.	.
	—	16.27	3517	216	—	0.07	8	114	.	.
	.	.	.	.	—	0.08	11	137	196	128
7	1.VIII.	9.55	1415	148	.	.	.	.	.	.
	—	8.53	1317	154	.	.	.	.	151	.
8	1.VIII.	18.24	3285	180	.	.	.	.	.	.
	—	8.72	1480	161	.	.	.	.	171	.
9	1.VIII.	32.71	4996	153	.	.	.	.	.	.
	—	45.90	6441	141	.	.	.	.	147	.
10	1.VIII.	13.21	2229	170	25.VIII.	0.06	3	50	170	50
11	1.VIII.	16.28	1678	102	2.VIII.	0.24	2	8	.	.
	—	15.28	1536	100	—	0.23	1	4	101	6

Table 5 (continued).

No.	Garden soil				Sand				Siliques/g, mean	
	Date	Weight, g	Siliques	Siliques/g	Date	Weight, g	Siliques	Siliques/g	Garden soil	Sand
12	1.VIII.	12.94	995	76	25.VIII.	0.06	7	116	.	.
	—	21.97	1774	81	.	.	.	.	79	116
13	15.VIII.	3.72	454	126	.	.	.	.	126	.
14	1.VIII.	7.82	1031	132	.	.	.	.	.	.
	—	4.01	501	127	.	.	.	.	130	.
15	1.VIII.	20.49	2480	121	.	.	.	.	121	.
16	1.VIII.	15.48	1663	107	.	.	.	.	.	.
	—	14.20	1661	117	.	.	.	.	112	.
17	1.VIII.	8.55	1298	152	2.VIII.	0.08	5	83	.	.
	—	11.89	1934	162	.	.	.	.	157	83
18	1.VIII.	23.41	1755	75	.	.	.	.	.	.
	—	25.87	1904	74	.	.	.	.	75	.
19	1.VIII.	10.12	725	72	.	.	.	.	72	.
20	1.VIII.	3.23	664	206	.	.	.	.	206	.
21	15.VIII.	23.68	1225	52	25.VIII.	0.57	38	67	.	.
	25.VIII.	18.78	633	34	12.X.	0.25	16	64	43	66
21	.	.	.	.	30.VI.51	0.48	73	152	.	152
22	.	.	.	.	25.VIII.	0.38	5	13	.	.
	.	.	.	.	—	0.18	27	150	.	(84)

sepiments will remain. However, it is a condition for a reliable counting of the siliques that the plant should be definitively out of flower.

As a measure of the economy of the plant the quotient, number of siliques/total weight (g) was used. The total weight can only be accurate for the sand plants, as these ripen their relatively few siliques almost simultaneously. Waste of seed may thus be avoided. The garden soil plants, however, will always have shed no inconsiderable part of the seed before they are finally out of flower. The determination of the economic

quotient may thus be fully reliable for the sand plants, while the value found for the garden soil plants will always be a little too high, the weight of the seed and silique valves shed lacking in the total weight ascertained. Experience shows, however, that the weight of the seed is comparatively low in proportion to the weight of the axial parts of the plant.

The results of the weighings and the counting of the siliques are given in table 5. All the values for single plants are listed to show that the quotient seems to be fairly constant for each set. It appears from the table that the quotient for the garden soil series generally decreases somewhat with retarded flowering, even though exceptions may occur. As regards the sand series, the quotient seems to decrease more markedly with retarded flowering, though the material of late-flowering plants is too sparse to warrant general conclusions. The abundant material of early strains show at any rate quite unmistakably that the quotient for the sand plants ranges much higher than for the same strains under normal conditions of nutrition. A comparison of the two nutrition series of late-flowering strains seems rather to show a lower quotient for the starved plants, though irregularities may occur.

It should be mentioned here that the early sand plants are harmoniously developed. The flowering ceased early, the few siliques are well developed, and unsuccessful flowers are almost lacking. The late sand plants, however, are in most cases deformed, often acauline, with many flowers that have failed to develop. Thus it would seem that the lack of nutrition in the early-flowering plants induces a further shortening of the life cycle of the plant, which manifests itself by a sudden cessation of the flowering. Such a reaction is not recognisable in the late-flowering plants.

As to some single results for the garden soil series treated in the table it may be mentioned that the vigorous and fast-growing no. 9, which attained the highest total weight, 45.9 g, as regards its economic quotient falls entirely in place. On the other hand, the small and slow-growing no. 20 with a total weight of only 3.2 g, has a higher quotient than any other plant of the series. Lowest of them all is no 21, the only strain in which a greater number of plants did not reach the flowering stage. This strain may probably be assumed to occur in nature as winter annuals or possibly biennials; while the vegetative garden soil plants died the succeeding winter, one of the sand plants survived. This plant, which was fully mature already on June 30th, 1951, shows a quotient of 152, that is, more than twice that of the annual sand plants of the same set. Table 5 seems to show quite clearly that compared with the late-flowering ones, the early-flowering strains exhibit a particularly satisfactory



economy under unfavourable nutritive conditions. In the evaluation of this result it should probably be taken into consideration that the seed from which the plants for the experiments were raised had been sown in mull, not in sand. Already when transplanted to the sand culture, the experimental plants must have taken up some nourishment, and some soil particles may have adhered to the roots. If this reserve which they brought with them is on the whole of any importance for the development of the plants, the early plants must be assumed to be relatively more highly influenced by it than the late-flowering plants.

As a corrective to the 1950-cultures a simple supplementary cultivation experiment was therefore started in the spring of 1951, the seed being then sown directly in pots with sand. The pots employed were a little bigger than those used in the experiment of the previous year: upper surface measure 154 cm<sup>2</sup>, volume 1266 cm<sup>3</sup>. The experiments comprised only four of the previously cultivated strains, namely (cf. fig. 1).

No. 3, early-flowering (in flower 29.V, 1950)

No. 9, intermediary (in flower 12.VI, 1950)

No. 14, intermediary (in flower 20.VI, 1950)

No. 22, late-flowering (in flower 16.VII, 1950).

The seed was sown on April 22nd, and germinated satisfactorily; the seedlings grew rather close together in the pots. No thinning was carried out. A decimation of the plant stock gradually took place as a consequence of competition.

The following notes on flowering and ripening are at hand:

- 6.VI, no. 3: abundantly flowering.
- 26.VI, nos. 9 and 14: first flower buds visible.
- 2.VIII, no. 3: partially ripe.
- no. 9: abundantly flowering.
- no. 14: rather abundantly flowering.
- 12.VII, nos. 9 and 14: still abundantly flowering.
- no. 22: two individuals in flower.
- 1.VIII, no. 9: in the main ripe; still a few plants in flower.
- no. 14: ripe and still abundantly flowering.
- no. 22: generally flowering; earliest plants also with siliques.

The plants from half of each pot were removed gradually as they ripened, and the number of siliques counted. Owing to the dense growth a number of plants did not develop beyond the vegetative stage, so the not used half content of each pot was preserved for wintering. However,

Table 6. Supplementary sand culture experiments 1951  
(cf. the text).

No.	Number of plants			Siliques per fruiting plant	Siliques, total
	total	vegetative	fruiting		
3	72	5	67	5.1	340
9	67	8	61	4.0	243
14	105	26	79	2.4	193
22	58	39	19	5.2	99

all the vegetative plants died in the course of the winter. The result of the experiment is given in table 6.

The number of plants (i. e. only the controlled half content of the pot) varies somewhat, but must have regulated itself, the weaker plants having been choked. The non-flowering individuals were counted simultaneously with the harvesting of the last fructifying plants in each pot; as to the early-flowering strains all, as to the latest-flowering strains only a number of them, were extremely small and defective. Plants which were dead at the time of counting were not included in the counts.

As will be seen from the table, the number of fructifying plants as well as the number of siliques per plant are high for no. 3. No. 14 yielded a particularly large number of small and equally developed, fructifying plants, while no. 22 yielded relatively few, but more vigorous, fructifying individuals; no. 9 occupied an intermediate position in this respect. The experiment further shows that the final yield, here measured by the number of siliques (per areal unit), is comparatively high for the earliest flowering strain and decreases with retarded flowering.

In an experiment so planned and arranged that the number of individuals regulates itself by competition between the individuals of the same biotype, the total yield of seed per areal unit is probably independent of the number of individuals. SALISBURY (1942, p. 54) thinks, at any rate, to have found a proof of the probability that the reproductive capacity in nature under similar conditions is independent of the number of individuals. Thus this experiment seems to establish once more the success of the early-flowering strain under poor nutritive conditions. Accordingly the result of the experiments of the previous year can hardly be supposed to have been materially altered because the experimental plants were not started in sand.

## 7. Discussion.

As already fully elucidated by ALMQUIST (1921, 1926), and likewise appearing from the experimental results recorded here, the genetic constitution of *Capsella bursa pastoris* is subject to great local variation. The genetic differentiation and stabilisation of the local populations must in the course of time have taken place through a continuous selection of the type most suitable for the local conditions. This is what TURESSON (1922, p. 347) calls "the genotypical response of the species population to a definite habitat".

However, the material available for direct selection is the phenotypical manifestation of the genotype (STEBBINS, 1950, p. 105). It is a well-known fact that the phenotypical modifiability is highly different in the individual species and biotypes (TURESSON, 1922, ALMQUIST, 1926, p. 43, STEBBINS, 1950, p. 73). The less a population is open to modificative variability, the more radical will be the effect of the selection, and in extreme cases the result will be a strain which has specialised for a quite narrow ecological interval. In this way the sharply delimited, well defined, ecotypes will be established which to an essential extent enjoy the favour of the evolution-theorists. It seems to me, however, that such highly specialised types in an evolution-theoretical sense must be regarded as blindly ending lateral lines, as short shoots on the wide-branching tree of evolution.

Thus it seems to me that the momentary success of a strain as well as, especially, its future general success, must be determined by the degree of the individual modifiability within the strain. The more manifold the capacity of a given genotype to manifest itself in accordance with the different habitats, the greater will be its possibility for multiplication, and the greater material will be available for the possible mutation-inducing forces, whether of an internal or an external nature.

The mode of reaction of a plant in response to varying habitat conditions is probably in the last instance genetically conditioned. A genetic predisposition for modificative flexibility seems to be a very fortunate—perhaps an indispensable—acquisition for a taxon's success in an outer world with locally and temporally highly varying life conditions. In this respect attention should be called to the weed flora of our cultivated fields and waste places. A typical example is precisely *Capsella bursa pastoris* (cf. JESSEN and LIND, 1922–23, p. 223 f.).

The most important of the experimental results recorded here deserve a more detailed discussion, considering the points of view outlined above. The extremely early-flowering strains, nos. 1, 2, 3, and 4, exhibit a

pronounced adaptive tolerance to poor nutrition. Poor nutrition (sand culture) seems to induce a rapid cessation of the flowering, which ensures a fortunate economy. In the experimental results this is evident from the circumstance that the value of the quotient, number of siliques/total weight for the sand plants even greatly exceeds the corresponding value for the garden soil plants.

In this connection the provenance of these early strains is of interest. Nos. 1, 2, and 3 are derived from the garden behind the building for plant cultivation, the Royal Agricultural College, Rolighedsvej. The building was erected in 1858 as a home for sick, and up to 1926 the garden was laid out with walking paths for the patients, probably also in part as a vegetable garden. The garden paths were, no doubt, prepared with hoe and rake all summer, which must in the course of years have resulted in a selection of the weed stock to the benefit of small and early-flowering individuals. It would seem obvious that the late-flowering and tall individuals must have been particularly exposed to eradication through the constant activity of the gardener. The assumption as to the effectiveness of such a selection is supported by the circumstance that not only *Capsella*, but also *Poa annua* and *Senecio vulgaris* of the same provenance are represented by extremely early-flowering types parallel to the *Capsella* experimental plants (experiments not yet published).

A direct modificative adaptation to a short growing season, whether climatically or edaphically conditioned, or due to interference of culture (hoe, mattock), is *a priori* inconceivable. Modificative dwarfs with a satisfactory seed production will, as in the example mentioned, ensure the persistence of the stock until new combinations of genes and new mutations will possibly in the course of generations produce the genotype most suitable under the prevalent conditions.

No. 4 behaved in the experiment almost like the preceding ones. It is derived from Ivigtut, Greenland, that is, a place near the northern limit of the species, where a (genetic) adaptation to a short summer is, no doubt, a condition for life. Very likely various biotypes have been casually introduced by man in the course of time; but only the extremely early-flowering ones have been able to survive through seed propagation.

Nos. 5 and 6 are likewise fairly early-flowering. They are both derived from dry habitats exposed to the sun, where the water supply must be assumed to be often critical in the early summer. The experiments show that these strains, also, are tolerant to poor nutrition, in contrast to the later-flowering ones.

Thus, in general there seems to exist a positive correlation between



adaptation to a short period of growth on the one hand and poor nutrition on the other hand. This fact would seem to be of principal evolution-theoretical interest, as it may indicate one of the ways in which the short-lived geno-dwarfs have become differentiated, viz. through a selection within populations of poorly nourished pheno-dwarfs.

The phenological data of the experiments as a whole likewise deserve discussion. As to both series of nutrition it applies that there is a fairly close correlation between the total number of leaves and the flowering time (cf. fig. 2). As the rate of leaf development is reduced in the starved plants (table 1), the flowering is the more retarded the greater the constitutionally determined number of leaves. This is only true if the conditions of starvation do not give rise to a change of the number of leaves. As will appear from figs. 2 and 1, the various strains show highly different reactions in this respect. The majority of strains will, under sand culture, reduce the number of leaves to a greater or less extent as compared with the garden soil plants, but they do not generally start flowering just as early as these latter.

A special position is occupied by nos. 13 and 20, whose flowering is not retarded in sand culture; as to the latter, the sand plants are even the first to flower. These two strains are indigenous to the Alvar area of Öland.—Nearest to them comes no. 14 from a gravel-covered railway platform. As shown in table 4, the total weight of the garden soil plants of these numbers is remarkably low. From these results it may probably be concluded that the strains are so highly constitutionally predisposed for poor nutrition that they are only to a comparatively slight extent capable of utilising the favourable conditions which the garden culture may offer. The Alvar plants, in particular, present a marked dwarfish growth. In their external appearance they somewhat resemble *Hutchinsia petraea*, which likewise grows in the Alvar. We are here concerned with the final, highly specialised ecotype.

In his Öland flora, STERNER (1938, p. 107) mentions *Capsella bursa pastoris* as an archaeosynanthrope, and about its occurrence he says i. a., "bisweilen als Neophyt auf Felsenboden und an Meeresufer". If actually the *Capsella* of the Alvar is an anthropochorous plant, though of considerable age, which is probably most likely, it may give a hint as to the rate of differentiation into a morphologically as well as physiologically well defined ecotype. JESSEN and LIND (l. c., p. 226), however, dared not, apparently, reject the possibility that *Capsella* might be spontaneous in the Scandinavian countries. That such specialised types will rarely be found within a species which, like *Capsella bursa pastoris*, is mainly



associated with cultivated soil, must at the outset be taken for granted. But the Vridsloselille-strain, the experiment's no. 14, is evidently approaching such a specialisation. The most marked contrast to the Öland type is formed by nos. 11, 12, and 16, which show an exceedingly retarded flowering in sand, for a reduced growth rate as well as an increase of the final number of leaves contribute to a retarded flowering. These strains are derived from habitats which by their situation and vegetation indicate an abundant supply of nutrition (nitrate?). Their reaction to the sand culture can only be interpreted as an expression of a pronounced intolerance to poor nutrition.

The examples just discussed show that the construction and the life duration of the plants may be affected in entirely different ways by the state of nutrition. The type of reaction evidently depend to some extent on the nutritive conditions in the natural habitat of the plant. That the type of reaction is in itself independent of the constitutional construction and the life duration of the biotype, seems evident from a comparison between e. g. no. 7 and no. 22 (cf. figs. 1-2).

- No. 7. Habitat: Dry dike through luxuriant cultivated field; Constitutional early flowering. Reaction to sand culture: increase of number of leaves and relatively retarded flowering.
- No. 22. Habitat: Moist beach sand; constitutional late flowering. Reaction to sand culture: reduction of number of leaves and relatively advanced flowering.

These last-mentioned experimental results seem to warrant the following conclusion:

Biotypes which judging by their natural habitat show tolerance to poor nutrition react to sand culture by a reduction of the number of leaves, in which way compensation in time for a reduced growth rate is obtained, that is to say, the flowering time is regulated at the expense of the vegetative equipment. Result: The possibilities for an establishment of harmonious pheno-dwarfs are favourable.

And analogously:

Exacting biotypes react to sand culture by retaining or even increasing the number of leaves. A compensation in time for a reduced growth rate is excluded, and the flowering time cannot be regulated. Result: The possibilities for establishment of harmonious pheno-dwarfs are unfavourable.

In the above I have attempted to outline various types of constitutional and modificative adaptation to a single habitat factor on the basis

of the experimental results recorded. The unsorted material, as presented in the tables, shows, however, as was to be expected, that the results are sometimes obscure. But the relations between the plant and its environment are so complicated that one is satisfied merely to discern certain principles in Nature's grand, ever progressing experiment.

The Carlsberg Foundation has kindly granted me financial aid for carrying out the experiments. To the Trustees of the Foundation I wish to express my grateful acknowledgment.

### References.

- ALMQUIST, E., 1907: Studien über die *Capsella bursa pastoris* (L.). – Acta Horti Bergiani 4, 6.
- 1921: Studien über *Capsella bursa pastoris* (L.) II. – Ibid. 7: 42–95.
- 1926: Zur Artbildung in der freien Natur. – Ibid. 9: 28–75.
- JESSEN, K. og J. LIND, 1922–23: Det danske Markkruddts Historie. – Kgl. Danske Vidensk. Selsk. Skr., Naturvidensk. og Mathem. Afd., 8. Række, 8.
- SALISBURY, E. J., 1942: The reproductive capacity of plants. – London.
- STEBBINS, J. LEDYARD, Jr., 1950: Variation and evolution in plants. – New York.
- STERNER, R., 1938: Flora der Insel Öland. – Acta Phytogeographica Suecica. 9.
- TURESSON, G., 1922: The genotypical response of the plant species to the habitat. – Hereditas 3: 211–350.

## Is the Classification of Plant Communities either Possible or Desirable?

By D. A. WEBB

Much discussion has recently been raging, and is likely to continue for some time, on the classification of plant communities. For the most part it is rather technical, and consists in arguments as to the best mode whereby the community may be characterized—whether by characteristic species, dominant, facies, and so on. A few authors have concerned themselves with more fundamental aspects of the subject; but in general the important questions of what is classification and why do we classify things have not, in this context, received the attention which they deserve. It cannot be denied that the communication and the precisification of ideas in plant-sociology is at present sadly hampered by the lack of an agreed “system”. But system-building for its own sake is a sterile occupation, and amid the noise of battle between rival systems and principles there has been a tendency to overlook the obvious fact that the nature of a classificatory scheme should depend not only on the properties of the material of which it treats, but also on the purpose for which it is required.

It must first be emphasized that in any field of thought systematics—the reduction to order of a confusing array of facts—includes more than classification. It must comprise at least the following:—

- (1) An agreed technique of description.
- (2) An apparatus for the diagnosis and delimitation of units and classes.
- (3) An agreed nomenclature.
- (4) A method of classification.

Of these four ingredients (1) and (3) need only the briefest mention here. I would suggest, however, that a descriptive technique, standardized and recommended by an international authority, is at once the most

urgent and the most easily attainable objective in the whole field; and that it should be tackled before any further system-building is attempted. Nomenclature is, of course, a secondary matter and raises no vital question of principle. It need not be descriptive so long as it is precise; but it is important, if it is to win general acceptance, that it should not be misleading. We tolerate such misnomers in Linnean nomenclature as *Erica mediterranea* for a plant of the Atlantic coasts of Europe, because such misleading names form only a minute proportion of the whole. The majority of generic and specific names are either aptly descriptive or else are non-committal, and it is not worth while upsetting the system to correct the few misnomers that exist. Had the proportions been otherwise, however, LINNAEUS's nomenclature would have been scrapped or revised long ago. It is for this reason that a system which includes under *Potentilletalia caulescentis* a number of associations in a country 1000 km. distant from the nearest plant of *Potentilla caulescens* is, to say the least, unattractive. It may be perfectly logical, but it will always supply a gratuitous rallying-point for illogical objections to the system of which it forms part.

It is to the two remaining constituents of systematics—delimitation and classification—that this essay is devoted; and one of its main contentions is that until the problems of diagnosis and delimitation have been solved at least in part, attempts at elaborate and precise classificatory schemes are useless, for nothing is more out of place in science than pseudo-precision. The way in which this crucial problem is by-passed in nearly all recent discussion of sociological classification (even by those authors who are not committed to a particular classificatory system) is, indeed, rather disquieting.

For the ordinary taxonomist the problems of the diagnosis and delimitation of species are, though often troublesome, for the most part soluble. There are, it is true, the "difficult" critical groups such as *Hieracium*, *Sphagnum*, or the bacteria, in which even the most diligent search fails to reveal such constant discontinuities in the pattern of variation as lend themselves to the establishment of species. But these are a minority; if the plant kingdom consisted mainly of such groups systematics would have taken on a very different shape from its present one. The majority of species are guaranteed some measure of objectivity, stability and discriminability by the genetic pattern of cross-breeding within the species and reproductive isolation outside it. No comparable factor is available to stabilize plant communities. Indeed, a new problem in discrimination presents itself to the plant-sociologist, which the taxonomist

does not have to face: not only do his "species" (*i. e.* his associations considered as abstractions) grade insensibly into their neighbours, but also his "individuals" (*i. e.* the particular samples of a given association) are apt to merge into something else at their margins.

To say this is not to maintain that the attempt to recognize, name and describe plant communities is a futile one. But we shall succeed in this attempt only if we recognize frankly the very great difficulties inherent in the task. The fact is that the pattern of variation shown by the distribution of species among quadrats of the earth's surface chosen at random hovers in a tantalizing manner between the continuous and the discontinuous. If variation were continuous and all possible combinations of species could be realized, then the science of plant-sociology would be impossible. If variation were discontinuous, with a finite and manageable number of combinations of species which could be realized, and sharp boundaries between the communities, then a satisfactory taxonomy of communities would have been agreed on long ago, and no problem would exist. What we find, however, is that variation is continuous, but in some regions sudden and in others very gradual, and that there is a series of often striking but never perfect correlations between the distribution of different pairs of species. We find, in consequence, that there is a recognizable but very imperfect predictability of the remaining species of a community when some of the principal ones have been ascertained.

How, in these circumstances, should plant communities be defined and delimited? I have never seen the question discussed in general terms. How can we erect a system which does justice at once to the differences between an Irish and a Danish meadow and to the resemblances between them; and how, in either country are we to provide an apparatus for determining at what stage of inundation a community should no longer be called a meadow but a marsh?<sup>1)</sup>

The only way in which categories which form a continuum, without natural discontinuities such as those imposed by the genetic barriers between biological species, may be delimited, would seem to be by arbitrary and metrical boundaries. There is no particular objection to this if one realizes what one is doing. It is, for example, the only way in which the different regions into which we divide the world of colour may be delimited. Two people can argue for ever whether a given shade falls under green or blue, but it is easy to establish a convention that a parti-

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<sup>1)</sup> It makes no difference to the argument if one writes for meadow *Molinio-Arrhenatheretea* and for marsh *Scheuchzerio-Caricetea fuscae*.



cular wavelength forms the boundary, and thereby to put an end to all argument. Similarly one might agree on a certain minimum area-cover for a characteristic species, or group of species, as the criterion by which a quadrat would or would not fall within the definition of a particular association. I have never seen this attempted on any large scale, but I think that it should be. Indeed, it seems curious that plant-sociologists who accumulate such large masses of data in quantitative form should then rely merely on their faculty of recognition for sorting out the communities, instead of using a quantitative yardstick.

Doubtless many critics will wish to interrupt at this point with the objection that this difficulty of discrimination is imaginary, or at any rate secondary. Even if variation in vegetation is technically continuous, they will maintain, it is in practice so unevenly continuous that it is possible to treat it as if it were discontinuous. Over large areas it is slight, and then over a short distance it is very marked; in consequence the area occupied by ecotones is very small in comparison with that covered by the named communities. In other words there are states of relative ecological equilibrium (the associations) and of relative disequilibrium (the ecotones). One might compare the situation, according to this view, to a garden filled with bees; at any moment a few bees will be flying at random, or between one plant and another, but the great majority will always be in one of the "equilibrium" positions represented by an inflorescence. If, then, to use an oftquoted illustration of ASHBY's, an ecologist who stops his car and decides that here is a good place for taking quadrats has already taken, subjectively, the first step in classification, it is only the modest step of recognizing that the area is occupied by a "stable" and recurrent type of community and not by a rare and transitional one.

There is much truth in all this, but not enough to justify a general refusal to face the problems of delimitation. For a scientific taxonomy it is not enough to assure one's critics that with sufficient experience one can learn to recognize the units; there must be some means of defining them. Without this plant-sociology can only be a craft to which one is apprenticed, and not a science which one can learn. It is as if organic chemistry were conducted without analysis, simply by relying on the sense of smell. Not only is such a procedure uncommunicable; it is also unreliable. As the chemist may find himself one day handicapped by catarrh, so the plant-sociologist can suffer from the mental equivalent, and "recognize" communities which subsequent analysis fails to confirm as distinct or homogeneous entities.

I maintain, then, that until there has been elaborated a precise and objective machinery for determining to what community a given sample of vegetation belongs, it is idle to talk of the taxonomy of plant communities, or to attempt to classify them. Let us assume, however, that one day this problem will be solved. We shall then be in a position to start the work of classification. How should we set about it?

Nearly every biologist today is so deeply indoctrinated with the phylogenetic basis of the "natural" classification of organisms that he finds great difficulty in conceiving of classification in any other form. He assumes that it must be hierarchical, and he assumes that for each group of entities (such as plant communities) there is one classification and one only which is permanently satisfactory. But both these assumptions are quite unwarranted; and I believe that their influence on the classification of plant communities has been disastrous.

The simplest kind of classification consists merely in the establishment of two or more parallel classes—e. g. animal, vegetable and mineral. If we wish to proceed beyond this to a more complex scheme we can do so in either of two ways: we can establish new classes co-ordinate with those already set up, or we can establish new classes subordinate to them. As an example of the first procedure we could choose the classes Irish, English, Danish and so on: these would be equally applicable to animal, to vegetable and to mineral products. An object which had been classified by this procedure and labelled, say, "Irish animal" would have its position fixed in a two-dimensional grid. In this grid neither dimension is privileged over the other; it was only by chance that we mentioned composition first and nationality second. Our own interests and prejudices enter in here: if we are more interested in politics and geography than in natural history, we will regard the classification as Irish as the primary one and the classification as an animal as secondary. The biologist will of course take the opposite view. But from a detached and logical standpoint neither assumption is justified.

Our alternative procedure would have been to erect within each of our first classes, not superposed crosswise on them, a new series of classes, each of which would be meaningless except in the context in which it is established. Thus we would have vertebrates and invertebrates; fungi, algae and vascular plants; metals and non-metals. One cannot talk of an invertebrate mineral or a fungous animal; the system is hierarchical; each category finds its meaning only within the limits of the category next above it.

In order not to labour the point unduly the exposition has been

limited to two stages of classification. But of course the same applies to all subsequent stages, and we build up either a multidimensional grid or a hierarchy of many strata. The latter can be tabulated in the familiar form of a branching genealogical tree. The fact that the former cannot be effectively represented on paper is perhaps one reason why its possibilities are often overlooked.

The classification of organisms proceeds entirely on hierarchical methods—the text-book taxonomy, that is, which we believe to be approximately phylogenetic and therefore regard as “the” classification. But in other contexts organisms may be classified otherwise. In zoological and botanical gardens we have houses or beds for small mammals, tropical insects, hardy annuals, succulents. In two pots side by side may be found the cactus and the spiny *Euphorbia* which we are at such pains to relegate to two different volumes of our text-book, and different cupboards of our herbarium.

Purely for convenience, it will be said. True, but what other aim has classification than convenience? And although practical considerations of culture demand a special house for succulents, does not this house also fulfil an educational purpose? Is there not some advantage in seeing the spiny *Euphorbia* next to a cactus, as well as seeing it next to a leafy one? We must admit this, and even so we feel that the classification by genus and family is the more permanent and more fundamental. When the spiny *Euphorbia* comes into flower we feel inclined to say: “Ah-ha, this has shown you up in your true colours”.

The justification for this attitude is very real. It is a knowledge of the fact that the resemblance between two xeromorphs of different families, though real, striking and significant, is limited in its implications. It tells us little more than is on the surface. Whereas if we know that two plants are in the same genus, we have reason to believe that the resemblances between them will not be confined to, say, the floral structure on which the genus is founded, but will be almost unlimited in number, extending it may be, to the latex, the wood-anatomy, the structure of the pollen-grain and the number of the chromosomes. That is why we regard our “natural” classification as more real and fundamental than any other; it keeps together in the same division organisms which have not one but many features in common. But this almost endless reserve of resemblances which investigation can reveal among related organisms exists solely because it represents a common inheritance which divergent evolution has only had time to affect in a few particulars.

It is a great mistake, however, to suppose that a hierarchical classi-

fication applied to other material will always bring about the same happy result. Just as it is its genetic structure that gives to the species the peculiar distinctness which we cannot expect to find elsewhere in nature, so the fact that organisms are genetically related, and that their variability has arisen by divergent evolution, produces the peculiar pattern of correlation of variation which makes the natural phylogenetic classification so fruitful when once we have found it. If the material to be classified has obtained its diversity by evolutionary divergence in the same way as organisms have, then a phylogenetic and hierarchical classification will possess such outstanding advantages that it will always form the norm, and will only be supplanted temporarily for specific purposes. This is true, for example, of the languages of mankind. But if the units of the material are not genetically related, all the advantages of a hierarchical classification disappear, and its disadvantage—lack of elasticity—is thrown into sharp relief. If it is objected that many communities, at least of the same sere, are genetically related, a little reflection will show that this is only metaphorically true. The relation between an early and a late seral stage is analogous not to the relation between parent and offspring but rather to that between embryo and adult.

It follows, then, that plant communities should be classified multifactorially rather than hierarchically, if only for the reason that when we say of one community that it is 'related' to another we do not mean it is the same literal sense as when we say the same about two organisms. All we mean is that the resemblances between the two interest us at the moment more than the differences. But as our interest shifts, so does our concept of relatedness.

Consider merely four types of community—(1) heath, (2) bog, (3) chalk grassland and (4) calcareous marsh. (1) and (2) agree in their acid, peaty soil; (3) and (4) in their alkaline, mineral soil. But (1) and (3) are dry; (2) and (4) are waterlogged. Is (1) more nearly 'related' to (2) or to (3), and is (3) more nearly 'related' to (1) or to (4)? The questions are meaningless: one day one answer will strike us as more fruitful, the next day the other. The only satisfactory classification is one that we can hold one way up or the other according to our interest of the moment.

An analogy may be found in the classification of igneous rocks, which may from some points of view be regarded as communities of minerals. In every elementary manual of petrology a table is set out in the form of a two-dimensional grid with base/silica ratio along one co-ordinate and crystal-size along the other, and in this grid each main rock type finds its characteristic place. The point to notice is that it makes no difference



which way up the grid is printed. One cannot say that crystalline state is primary and chemical composition secondary; one may want to compare a gabbro with a dolerite on Monday and with a diorite on Tuesday: it is no more or less 'related' to one than to the other.

Or again consider the technique used by a war office in classifying its conscripts. For each man there is recorded his name, his county of origin, his age, his military unit, his technical qualification and so on. It would be possible to make these points the basis of different grades in a hierarchical classification, but it would be foolish, as none of them is more important or more fundamental than the rest. Instead, the data are all recorded on a punched card, and this can then be sorted and re-sorted for whatever qualities we wish, in whatever order we wish. And only a system of multifactorial recording which is capable, if we wish, of being carried on a punched card, can form a satisfactory basis for the classification of plant communities. The essential point is the orderly recording of the independent variables by means of suitable symbols: classification then becomes a temporary process which can be adapted to the needs of the moment.

The fact that in plant communities not all the factors which are responsible for variation are independent does not affect the issue. So long as a considerable number are independent, then it makes little difference whether there exist as well some others which are correlated. And if we consider the main variable factors of the environment of plants, we find that a large number of them are capable of independent variation within wide limits. For example:—

Wind exposure.  
Insolation.  
Nitrate content of soil.  
Water capacity of soil.  
Days of snow cover.

Here, without going further, is the basis of a five-dimensional grid.

One cannot think coherently about a large number of objects without classifying them mentally; and most people's minds are incapable of handling a classification of more than two stages except in hierarchical terms. But when the variables are independent we must retain the power to make and unmake our hierarchies as we wish, to reveal different kinds of relatedness. The counters must be shuffled round for many years still before we can find which is the pattern that is most significant; and never will any one pattern display all the facts at once.



This is no counsel of despair. To work out a technique for a lucid and concise description and an unambiguous specification of communities, and for coding, filing, sorting and displaying them is difficult but surely possible: it is not only desirable, but necessary. But to accumulate an ever-growing list of names without precise specification; to arrange these in a hierarchy according to a unspecified principle of relatedness which can, at best, be one out of several possibles; to declare that this is the one and only system of classification and to seek to have it imposed by international authority—this surely is not science but scholasticism out of place.

## Nogle indslæbte Planter i Pedersborg ved Sorø

Af K. WIINSTEDT

Det er sparsomt, hvad der foreligger i dansk botanisk Litteratur om indslæbte Planter i Danmark. Foruden JOH. LANGE's Publikationer om italienske Planter fundet ved Thorvaldsens Museum i København (1845), samme Forfatters mange Oversigter over de i Danmark iagttagne sjældne eller for den danske Flora nye Arter i Botanisk Tidsskrift, hans Oversigt over de i nyere Tid til Danmark indvandrede Planter (1896) og hans to Beretninger sammen med H. MORTENSEN i samme Tidsskrift (i Fortsættelse af de tidligere nævnte), har kun C. H. OSTENFELD (1895) taget Initiativet til at videreføre disse værdifulde Beretninger; senere sammen med Lægen OTTO MØLLER (1902), efter at denne havde publiceret sin Oversigt over de siden 1894 i Danmark indslæbte Planter (1898). Men alle disse Publicationer rummer imidlertid kun forholdsvis faa Meddelelser om indslæbte Planter og tager ikke Forekomsten paa enkelte Lokalteter op til nærmere Behandling. Kun H. MORTENSEN meddeler om nogle udsaaede Planter ved Sønder søen (1868), men hvad han fandt der af sammen med Græsfrø indslæbte Planter, har kun ringe Relation til, hvad der samtidig kunde findes indslæbt f. Eks. paa de talrige Ruderatpladser i og omkring København og i de større Provinsbyer. Først i de mange smaa Bidrag til den danske Flora, som C. H. OSTENFELD publicerede i Botanisk Tidsskrift ofte ledsaget af Bestemmelsesnøgler til Arterne inden for en enkelt Slægt, nævnes en Del af de i Begyndelsen af dette Aarhundrede indslæbte Planter. I 1909 meddeler Forf. af dette Arbejde, hvad der kan findes indslæbt paa en begrænset Plads af et enkelt Firma i Horsens (1909) og fortsætter med at publicere Fund i nye Bidrag til den danske Flora i forskellige Bind af Bot. Tidsskr. og med enkelte Artsnøgler. Desuden kan nævnes SVEND ANDERSEN's faatallige Liste over indslæbte Planter paa Spritfabrikens Tomt i Aalborg (1935). Endelig er der i KNUD JESSEN's og JENS LIND's store Afhandling om Markkruddes Historie i Danmark behandlet enkelte indslæbte Planter (1923).

Naar der blandt floristisk indstillede Botanikere endnu hersker en vis Interesse for at opsøge indslæbte Planter og herbarisere disse, skyldes det ikke alene det spændende Moment, der ligger i at konstatere, at denne eller hin udenlandske Art er fundet indslæbt paa en Ruderatplads, en Havneplads eller paa et Jernbaneterræn, maaske ny for den danske Flora; men bag denne Opfattelse kan tillige ligge den praktiske Sag, at en eller flere af disse indslæbte Planter maaske kunde blive et for vort værdifulde, opdyrkede og værnede Kulturomraade farligt Ukrudt, som det gælder om at udrydde, inden det faar Tid til at akklimatisere sig. Denne Opfattelse var især fremherskende i Begyndelsen af forrige Aarhundrede, hvor alt var sat ind paa at opbølge Landets slette finansielle Forfatning, og som gav sig Udslag i C. F. HORNEMANN: „Forsøg til en dansk oeconomisk Plantelære“, hvis sidste Udgave udkom i 1821. Det kan vel ikke nægtes, at nogle i Slutningen af Aarhundredet indslæbte Arter synes at skulle blive Ukrudt af noget foruroligende Karakter; af saadanne kan nævnes: *Erigeron canadensis*, *Matricaria matricarioides*, *Senecio vernalis*, de to *Galinsoga*-Arter og *Ambrosia psilostachya*. Hvor den sidste er kommet ind paa Agerjord, er den saa godt som uudryddelig paa Grund af sin vegetative Formering.

Indslæbningen af fremmede Planter til Danmark er sandsynligvis begyndt saa tidligt som ved Agerbrugets Opstaaen. De fleste af de nu paa vore Stubmarker hyppige Ukrudsplanter er sikkert indkommet for mange Aarhundreder siden med fremmed Kloverfrø, Græsfrø og Sædekorn. Da Floristiken fra Midten af det forrige Aarhundrede og indtil Begyndelsen af dette var den alt overvældende botaniske Faktor med Systematiken i Højsædet, og samtidig Handelsimporten voksede, og fremmed Plantefrø indførtes mere og mere til Brug i teknisk Øjemed, steg Indslæbningen af Planter fra fjerne Egne i betydelig Grad. Omkring 1910 kunde saaledes paa en Ruderatplads i København findes følgende fra Sydeuropa og Amerika indslæbte Arter: *Amaranthus retroflexus*, *Brassica elongata* v. *armoracioides*, *Berteroa incana*, *Dipsacus silvestris*, *Echinochloa Crus-galli*, *Hyoscyamus niger*, *Iva xanthiifolia*, *Kochia scoparia*, *Lepidium densiflorum*, *L. Draba*, *Malva parviflora*, *Panicum capillare*, *P. miliaceum*, *Phalaris canariensis*, *Ph. paradoxa*, *Polygonum patulum*, *Salvia verticillata*, *Setaria italica*, *S. viridis*, *Silene dichotoma*, *Sisymbrium altissimum*, *S. Loeselii*, *S. orientale*, foruden de i Fuglefrø forekommende *Cannabis sativa* og *Guisotia Abyssinica*. – Da Soyakage-Industrien senere hentede sit Materiale fra Østasien, indslæbtes paa vore Ruderatpladser, især i København, en Mængde østasiatiske Arter, deriblandt den ejendommelige tornede *Polygonum Bungeanum* TURCZ. sammen med *Glycine*

*hispida* (Soya), der aldrig naaede at modne sine Bælge, men disse og andre maatte forsvinde under den sidste Verdenskrig, da Importen fra Østasien standsede. – Andre indslæbtes fra Sydamerika, men især fra Middelhavslandene med Sydfrugt- og Korkimporten. Københavns Frihavn blev et sandt Eldorado for de Florister, der gik paa Jagt efter nye danske Planter, men ogsaa denne Lokalitet er nu paa stærk Retur.

De gamle Ruderatpladser i Byerne er ogsaa saa godt som forsvundet paa Grund af den mere og mere praktiske Anordning af Dagrenovationens Destruering. Men hvor kan da i vore Dage Indslæbning finde Sted af nye Arter og Genindslæbning af de af vort Vinterklima udslettede Arter finde Sted? Svaret maa da blive Ruderatpladser i smaa Provinsbyer, Høsegaarde, hvor Froaffald udkastes som Foder, og Pladser, hvor der oplagres importerede Trævarer til Brug for en eller anden Industri, deriblandt Korkindustrien. Efterfølgende Fortegnelse over indslæbte Planter er saaledes hentet fra en Plads, hvor et Firma forarbejder Kork i industrielt Øjemed. Den er beliggende lidt nord for Sorø i Pedersborg og er blevet undersøgt af følgende fire Florister: Lærer EGEDE JENSEN i Sorø, Lærer EVALD LARSEN i Ringsted, Lærer INGERSLEV HANSEN i Nykøbing F. og Lærer S. M. RASMUSSEN i Roskilde. Disse Florister har indsendt deres Fund til Revision til Botanisk Museum og har derigennem givet mig den Opgave at bestemme Planterne, som alle viste sig at høre hjemme paa den spanske Halvø og i Marokko. En Henvendelse til Firmaet „Sorex, Teknisk Korkindustri” i Pedersborg, bekræftede da ogsaa, at det kun importerede Kork fra disse Landomraader. Opdagelsen af Pladsen som floristisk interessant blev først gjort i 1951, og Fundene kan saaledes alle dateres til de sidste tre Aar. Der kan derfor ikke siges noget sikkert om, hvorvidt enkelte Arter har formaat at akklimatisere sig og sætte spiredygtige Frø, men den vedvarende Import vil utvivlsomt stedse forsyne Pladsen med ny eller periodisk forsvundne Arter. Mange af de indsendte Planter var tidligere fundet af afdøde Direktør SVEND ANDERSEN i Københavns Frihavn paa Kajen, hvor Korkskibene lægger til, men adskillige var nye for Floraen. – Der savnes endnu en Fortegnelse over de i nyere Tid indslæbte Planter i Danmark. Deres Tal løber op til mellem syv og otte Hundrede, der saa godt som alle er repræsenterede i Botanisk Museums specielle Ruderatherbarium. Nærværende Liste er saaledes kun et ringe Bidrag til Belysning af vor indslæbte Flora, men kan formodentlig have vegetations-historisk Interesse.

Følgende Forkortelser er anvendt i Listen. E. J. = EGEDE JENSEN. – E. L. = EVALD LARSEN. – I. H. = INGERSLEV HANSEN. – S. M. R. = S. M. RASMUSSEN.

Slægterne og Arterne er af praktiske Hensyn i alfabetisk Orden.

En \* betegner de for Floraen ny Arter.

## I. Monocotyledones.

### Gramineae:

*Brachypodium distachyum* (L.) PB. – E. J. 53. \**Briza minor* L. – E. J. 53. *Bromus madritensis* L.–E.J. 53. *Cynosurus echinatus* L.–E.J. 53. *Digitaria sanguinalis* SCOP.–E.J. 53. *Gastridium ventricosum* SCH. et THELL.–E. J. 53. \**Trisetum Baregense* LOFF. et MIEG.–E. J. 53. *Vulpia ciliata* LK.–I. H. 52. *V. Myurus* (L.) C. C. GMEL. 52.

## II. Dicotyledones – Choripetalae.

### Amaranthaceae:

*Amaranthus albus* L.–I. H. 53. *A. blitoides* S. WATS.–I. H. 52. *A. deflexus* L.–E. J. 52. *A. lividus* L.–I. H. 53. *A. paniculatus* L.–E. J. 52. *A. angustifolius* LAMM.–E. J. 51.

### Caryophyllaceae:

\**Herniaria hirsuta* L. var. *gracilis* LGE.–E. L. 53. \**Polycarpon tetraphyllum* L.–E. J. 53. *Silene noctiflora* L.–E. J. 53.

### Chenopodiaceae:

*Chenopodium ambrosioides* L.–E. J. 52. *C. murale* L.–E. J. 52. *C. opulifolium* SCHRAD.–J. H. 53.

### Cruciferae:

\**Coronopus didymus* SM.–E. J. 53. *Diploaxis muralis* (L.) D.C.–I. H. 53.

### Euphorbiaceae:

*Euphorbia exigua* L.–E. J. 53.

### Fumariaceae:

*Fumaria muralis* SOND.–E. J. 52.

### Lythraceae:

*Lythrum hyssopifolia* L.–E. J. 53.

### Malvaceae:

*Malva crispa* L.–E. J. 53. *M. parviflora* L.–E. J. 53.



## Papilionaceae:

*Medicago hispida* GAERTN.—E. J. 53. \**Scorpiurus muricata* L.—E. J. 53.  
*Trifolium elegans* SAVI.—E. J. 53. *T. nigrescens* VIV.—E. J. 53. *T. subterraneum* L.—E. J. 53. *T. tomentosum* L.—E. J. 52. *Vicia peregrina* L.—E. J. 52.

## Polygonaceae:

*Polygonum arenarium* W. et K.—E. J. 51. *P. aequale* LINDM.—E. J. 53.

## Portulacaceae:

*Portulacca oleraceae* L.—E. J. 53.

## Ranunculaceae:

\**Ranunculus muricatus* L.—E. J. 52.

## Umbelliferae:

*Ammi Visnaga* LAM.—I. H. 52. *Bupleurum Odontitis* L.—E. J. 53.

## Zygophyllaceae:

*Tribulus terrestris* L.—E. J. 53.

## III. Dicotyledones – Sympetalae.

## Borraginaceae:

*Heliotropium europaeum* L.—E. J. 52.

## Campanulaceae:

*Specularia Speculum-Veneris* TANF.—E. J. 52.

## Compositae:

*Anacyclus radiatus* LOIS.—E. J. 53. \**Andryale integrifolia* L.—E. J. 53.  
*Anthemis mixta* L.—E. J. 52. *Artemisia annua* L.—E. J. 53. *Carthamus Oxyacantha* M. B.—E. J. 52. *Centaurea Calcitrapa* L.—E. J. 52. *Erigeron Bonariense* L.—E. J. 52. *Pulicaria arabica* CASS.—E. J. 53. *Scolymus hispanicus* L.—E. J. 52. *Tagetes erectus* L.—E. J. 52. *Tolpis barbata* GAERTN. E. J. 52.

## Labiatae:

*Mentha Pulegium* L.—E. J. 52. *Salvia verticillata* L.—E. J. 53.

## Plantaginaceae:

*Plantago Coronopus* L.—S. M. R. 53. *P. indica* L.—E. J. 53. *P. Lagopus* L.—E. J. 53.

## Primulaceae:

*Anagallis femina* MILL.—S. M. R. 53.

## Scrophulariaceae:

\**Linaria Pelisseriana* (L.) MILL.—E. J. 53. *L. spuria* MILL.—E. J. 53.

## Solanaceae:

*Solanum luteum* MILL.—I. H. 52. *S. Sarrachoides* SENDT.—E. J. 52.

## Verbenaceae:

*Verbena supina* L.—E. J. 52.

## Litteratur.

ANDERSEN, SVEND, 1935: En Adventivflora på den nedrevne Spritfabriks Tomt i Ålborg. Bot. Tidsk. 43.

JESSEN, KNUD og LIND, 1923: Det danske Markukrudts Historie. Vid. Selsk. Skr. 8, 8.

LANGE, J., 1845: En uventet Tilvækst til den danske Flora. Dansk Ugeskrift.

— 1865, 66, 67, 68 og 72: Oversigt over de i Danmark iagttagne sjældne eller for den danske Flora nye Arter. Bot. Tidsk. 2, 3 og 5.

— 1869: Oversigt over de i nyere Tid til Danmark indvandrede Planter med særlig Hensyn til Tiden for deres Indvandring. Bot. Tidsk. 20.

— og MORTENSEN, 1872, 78, 79, 83 og 84: Oversigt over de i Danmark fundne sjældnere eller for den danske Flora nye Arter. Bot. Tidsk. 10 og 14.

MORTENSEN, H., 1868: Sønder søens Vegetation, et Bidrag til den nordsjællandske Flora. Bot. Tidsk. 2.

MØLLER, OTTO, 1902: Oversigt over de siden 1894 i Danmark indslæbte Planter. Bot. Tidsk. 22.

— og OSTENFELD, 1902: De i de senere Aar i Danmark iagttagne Findesteder for mindre almindelige Karplanter. I Pteridophyta og Monocotyledones. Bot. Tidsk. 24.

OSTENFELD, C. H., 1895: Nogle ny-indslæbte Planter. Bot. Tidsk. 19.

WIINSTEDT, K., 1909: Optegnelser fra en Ruderatplads. Bot. Tidsk. 29.

## Indholdsfortegnelse

E. BILLE-HANSEN: The Danish species of <i>Geoglossum</i> and related genera . . . .	7
N. FABRITIUS BUCHWALD: <i>Ciboria Batschiana</i> (Zopf) Buchw. (Syn. <i>Sclerotinia pseudotuberosa</i> (Rehm)Rehm). Contribution to the discussion of the nomenclature of the species . . . . .	19
TYGE W. BÖCHER: Natural populations of the <i>Pulsatilla</i> in Zealand . . . . .	33
F. BÖRGESEN: Two new species of <i>Laurencia</i> from Mauritius . . . . .	48
TYGE CHRISTENSEN: Some considerations on the phylogeny of the Bryophyta. . . . .	53
M. SKYTTE CHRISTIANSEN: <i>Nanostictis</i> , a new genus of scolecosporous Discomycetes . . . . .	59
ERNST FLOTO: Iagttagelser over <i>Smyrnum perfoliatum</i> L. (Summary: Observations on <i>Smyrnum perfoliatum</i> .) . . . . .	66
P. GELTING: The <i>Rhizocarpon</i> species with peltate areoles occurring in Europe and North America . . . . .	71
K. GRAM: The lifeform and growth of <i>Artemisia campestris</i> L. . . . .	93
JOHS. GRÖNTVED: <i>Galium boreale</i> L., new to Greenland . . . . .	98
O. HAGERUP: Autogamy in some drooping <i>Bicornes</i> flowers. . . . .	103
L. HARMSSEN: Om <i>Polyporus caesius</i> og <i>Ditiola radicata</i> som tømmer-svampe. (Summary: <i>Polyporus caesius</i> and <i>Ditiola radicata</i> as timber fungi.) . . . . .	117
ERIC HULTÉN: A new <i>Oxytropis</i> species from Alaska . . . . .	124
H. NILAUS JENSEN: Universitetets botaniske haver. Historie, formål og tilstand . . . . .	126
H. JONASSEN: Dating of sand-drift east of Ulfborg . . . . .	136
MAUNO J. KOTILAINEN: The <i>Stratiotes</i> lakes in Kittilä (Finnish Lapland) as a floristic and quaternary problem. . . . .	141
MOGENS KØIE: Characterization of plant groups by area coverage. . . . .	157
JOHAN LANGE: Dansk botanisk topografi og dens forhold til Kyllings Viridarium. (Summary: Danish botanical topography and its relation to the Viridarium of P. Kylling.) . . . . .	172
MORTEN LANGE & LISE HANSEN: The phylogenetic position of Agaricales. . . . .	185
ARNE LARSEN: Bornholms botaniske seværdigheder . . . . .	195
KAI LARSEN: Cytotaxonomical studies in <i>Lotus</i> . I. <i>Lotus corniculatus</i> L. sens. lat. . . . .	205
BERTIL LINDQUIST: Notes on <i>Cercidiphyllum magnificum</i> Nakai . . . . .	212
ANDERS MUNK: Notes on some Hypocreales recently found in Denmark. . . . .	220
D. MÜLLER: Vørsø set fra luften. . . . .	230
F. H. MØLLER: The genus <i>Leucopaxillus</i> in Denmark . . . . .	233
E. STEEMANN NIELSEN: On the preference of some freshwater plants in Finland for brackish water . . . . .	242
ROLF NORDHAGEN: Some new observations concerning the geographic distribution and the ecology of <i>Arenaria humifusa</i> Wg. in Norway as compared with <i>Arenaria norvegica</i> Gunn. . . . .	248

CARSTEN OLSEN: Hvilke betingelser må være opfyldte, for at <i>Helodea canadensis</i> kan opnå den optimale udvikling, der er årsag til dens massevisse optræden i naturen? (Summary: What are the conditions of optimum development enabling <i>Helodea canadensis</i> to grow profusely in nature?).....	263
HUGO OSVALD: Sloping mires in north-western Norway .....	274
JOHS. BOYE PETERSEN & J. BENTH HANSEN: Electron microscope observations on <i>Codonosiga botrytis</i> (Ehr.)James-Clark .....	281
A. E. PORSILD: The North American races of <i>Saxifraga flagellaris</i> Willd.....	292
KNUD RAHN: Experimental and cytological studies in <i>Plantago media</i> .....	300
ELISABETH SCHIEMANN: Die Geschichte der Kulturpflanzen im Wandel der biologischen Methoden.....	308
C. SKOTTSBERG: Antarctic flowering plants.....	330
THORVALD SØRENSEN: Adaptation of small plants to deficient nutrition and a short growing season. Illustrated by cultivation experiments with <i>Capsella bursa pastoris</i> (L.) Med.....	339
D. A. WEBB: Is the classification of plant communities either possible or desirable? .....	362
K. WIINSTEDT: Nogle indslæbte planter i Pedersborg ved Sorø.....	371

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Redaktion: *Morten Lange*.

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Bindet udkom 29. november 1954.

## Artsregister

(Arter i floralister, i sociologiske undersøgelser eller kun forbigående nævnt i teksten er ikke medtaget).

- Allium oleraceum*, 177.  
*Andromeda polifolia*, 109 f, 114\*, 177.  
*Andryale integrifolia*, 375.  
*Anemone apennina* var. *pallida*, 201\*.  
*Apium graveolens*, 182.  
*Arctostaphylos alpina*, 110\*, 111.  
     — *uva-ursi*, 108 f\*.  
*Arenaria ciliata* ssp. *pseudofrigida*,  
     257\*, 260 f.  
     — *humifusa*, 248 ff\*.  
     — *norvegica*, 248 ff\*.  
*Arum maculatum*, 179.  
*Artemisia campestris* ssp. *eucampestris*,  
     93 ff\*.  
*Asplenium ruta-muraria*, 182.  
*Barya parasitica*, 220 ff\*.  
*Bertia moriformis*, 221\*.  
*Blechnum spicant*, 182.  
*Botrychium lunaria*, 182.  
*Braya linearis*, 255, 256\*, 257\*.  
*Briza minor*, 374.  
*Calla palustris*, 179.  
*Campanula glomerata*, 181.  
     — *rapunculus*, 181.  
*Capsella bursa-pastoris*, 339 ff.  
*Cassiope tetragona*, 111 f\*.  
*Cephananthra longifolia*, 181.  
*Ceratophyllum demersum*, 150\*, 244.  
*Cercidiphyllum japonicum*, 212 ff\*.  
     — *magnificum*, 212 ff\*.  
*Ciboria batschiana*, 19 ff, 30\*.  
     — *pseudotuberosa*, 22, 23\*, 26\*.  
*Cnidium dubium*, 182.  
*Codonosiga botrytis*, 281 ff\*.  
*Colobanthus crassifolius*, 333\*, 334 ff.  
*Coronopus didymus*, 374.  
*Corynetes atropurpureus*, 9.  
     — *arenarius*, 10.  
*Debaryella*, 228.  
*Debaryella gracilis*, 226 f\*.  
*Deschampsia antarctica* 331 ff\*.  
     — *parvula*, 335, 336\*.  
*Dipsacus silvester*, 182.  
*Ditila radicata*, 120\*, 121 f\*.  
*Dryopteris thelypteris*, 183.  
*Equisetum telmateia*, 183.  
*Erica arborea*, 113.  
     — *carnea*, 110\*, 113.  
     — *mediterranea*, 110\*, 113.  
     — *tetralix*, 177.  
*Eriophorum alpinum*, 179.  
*Eryngium maritimum*, 182.  
*Flammulina velutipes*, 191\*.  
*Galium aparine*, 101.  
     — *boreale* 98 ff\*.  
     — *brandegei* 101.  
     — *pumilum*, 102.  
     — *triflorum*, 101.  
     — *uliginosum*, 101.  
*Geoglossum cookeianum*, 15\*, 16.  
     — *fallax*, 12, 13\*.  
     — *glabrum*, 15\*, 16.  
     — *glutinosum*, 12.  
     — *littorale*, 17.  
     — *nigrum*, 13\*, 14.  
     — *peckianum*, 12.  
     — *simile*, 15\*, 16.  
     — *starbaeckii*, 13\*, 14.  
*Geranium silvaticum*, 179.  
*Gymnadenia conopsea*, 199\*.  
*Helodea canadensis*, 244 ff.  
*Herniaria hirsuta* var. *gracilis*, 374.  
*Hypericum hirsutum*, 178.  
     — *pulchrum*, 178.  
*Lathyrus silvester*, 176.  
*Laurencia subcolumnaris* 48 ff\*.  
     — *verruculosa*, 50 ff\*.  
*Lentinus lepideus*, 191\*.



- Lentinus ursinus*, 191\*.  
*Leucopaxillus alboalutaceus*, 239\*,  
     240 f.  
     — *amarus*, 239 f.  
     — *giganteus*, 235 f.  
     — *rhodoleucus*, 237 f\*.  
     — *spinulosus*, 236 f\*.  
     — *tricolor*, 238 f\*.  
*Levisticum officinale*, 182.  
*Limonium humile*, 180.  
*Linaria pelisseriana*, 376.  
*Lotus corniculatus*, 205 ff.  
     — — *var. alpinus*, 207.  
     — *tenuis*, 208.  
     — *uliginosus*, 208.  
*Melilotus dentatus*, 175.  
*Microglossum olivaceum*, 9.  
     — *viride*, 9.  
*Monotropa hypopitys*, 113, 114\*.  
*Myriophyllum spicatum*, 242 ff.  
*Najas flexilis*, 144 ff\*.  
*Nanostictis peltigerae*, 59 ff\*.  
*Narcissus pseudonarcissus*, 176.  
*Nectria cosmariospora*, 225\*.  
     — *magnusiana*, 225\*.  
     — *modesta*, 224 ff\*.  
     — *sanguinea*, 225\*.  
*Nuphar pumilum*, 202\*.  
*Panellus mitis*, 190\*.  
     — *ringens*, 190\*.  
     — *serotinus*, 190\*.  
     — *stypticus*, 190\*.  
*Panus rudis*, 191\*.  
*Paxillus panuoides*, 191\*.  
*Pernettya macrostigma*, 115.  
*Peziza glandicola*, 27.  
*Phyllodoce coerulea*, 111, 112\*.  
*Phyllotopsis nidulans*, 190\*.  
*Plantago media*, 300 ff\*.  
*Poa annua*, 337.  
*Polycarpon tetraphyllum*, 374.  
*Polygonum bistorta*, 178.  
*Polyporellus brumalis*, 190\*.  
*Polyporus caesius*, 117 ff\*.  
*Potamogeton filiformis*, 151\*.  
     — — *× vaginatus*,  
         151\*.  
     — *lucens*, 150\*.  
*Potamogeton rutilus*, 153\*.  
     — *zizzii*, 150\*.  
     — *zosterifolius*, 151\*.  
*Primula farinosa*, 177.  
*Pulsatilla pratensis*, 33 ff\*.  
     — — *var. duplex* 43\*, 44.  
     — — *f. johanssonii*, 36\*,  
         38, 39\*.  
     — *vulgaris*, 33 ff, 40\*.  
     — — *f. bogenhardiana*, 44.  
     — — *ssp. germanica*, 43.  
*Pyrola media*, 114\*, 115.  
     — *minor*, 114 f, 180.  
     — *rotundifolia*, 198\*.  
*Ophioglossum vulgatum*, 182.  
*Ophionectria cerea*, 222 ff\*.  
*Oxycoccus quadripetalus*, 105\*, 107,  
     177.  
*Oxytropis glaberrima*, 124 f\*.  
*Ranunculus muricatus*, 375.  
*Rhizocarpon arctogenum*, 72 ff, 81 ff\*.  
     — *bolanderi*, 71 ff, 84 ff\*.  
     — *leptolepis*, 72 ff, 85\*, 87 ff.  
     — *rittokense*, 72 ff, 89 ff\*.  
*Sagittaria sagittifolia*, 180.  
*Samolus valerandi*, 177.  
*Saxifraga flagellaris*, 292.  
     — *ssp. flagellaris*, 293\*, 295 ff.  
     — — *megistantha*, 293, 296 ff.  
     — — *mucronulata*, 293\*, 296 ff.  
     — — *platysepala*, 293\*, 295 ff.  
*Sclerotinia batschiana*, 29.  
     — *pseudotuberosa*, 19.  
*Scorpiurus muricata*, 375.  
*Smyrniolum olusatrum*, 66, 68\*.  
     — *perfoliatum*, 66 ff\*.  
*Spiranthes autumnalis*, 200\*.  
*Stictis radiata*, 63 f\*.  
*Stratiotes aloides*, 141, 142\*, 146\*.  
*Trichoglossum hirsutum*, 17.  
     — *tetrasporum*, 17.  
     — *variabile*, 18.  
     — *walteri*, 18.  
*Triglochin palustre*, 180.  
*Trisetum baregense*, 374.  
*Vaccinium myrtillus*, 105\*, 106.  
     — *uliginosum*, 104 ff\*, 112\*.  
     — *vitis-idaea*, 107\*.



# INDHOLD

<i>E. Bille-Hansen</i> : The Danish species of <i>Geoglossum</i> and related genera .....	7
<i>N. F. Buchwald</i> : <i>Ciboria Batschiana</i> (Zopf) Buchw. ....	19
<i>Tyge W. Böcher</i> : Natural populations of <i>Pulsatilla</i> in Zealand .....	33
<i>F. Børjesen</i> : Two new species of <i>Laurencia</i> from Mauritius .....	48
<i>Tyge Christensen</i> : Some considerations on the phylogeny of the Bryophyta .....	53
<i>M. Skytte Christiansen</i> : <i>Nanostictis</i> , a new genus of scolecosporous Discomycetes...	59
<i>Ernst Floto</i> : Iagttagelser over <i>Smyrnum perfoliatum</i> L. ....	66
<i>P. Gelting</i> : The <i>Rhizocarpon</i> species with peltate areoles in Europe and N. America.	71
<i>K. Gram</i> : The lifeform and growth of <i>Artemisia campestris</i> L. ....	93
<i>Johs. Grøntved</i> : <i>Galium boreale</i> L., new to Greenland .....	98
<i>O. Hagerup</i> : Autogamy in some drooping <i>Bicornes</i> flowers. ....	103
<i>L. Harmsen</i> : Om <i>Polyporus caesius</i> og <i>Ditiola radicata</i> som tømmer svampe .....	117
<i>Eric Hultén</i> : A new <i>Oxytropis</i> species from Alaska .....	124
<i>H. Nilas Jensen</i> : Universitetets botaniske haver .....	126
<i>H. Jonassen</i> : Dating of sand-drift east of Ulfborg. ....	136
<i>M. J. Kotilainen</i> : The <i>Stratiotes</i> lakes in Kittilä .....	141
<i>M. Koie</i> : Characterization of plant groups by area coverage. ....	157
<i>J. Lange</i> : Dansk botanisk topografi og dens forhold til Kyllings Viridarium. ....	172
<i>M. Lange &amp; Lise Hansen</i> : The phylogenetic position of Agaricales .....	185
<i>Arne Larsen</i> : Bornholm botaniske seværdigheder. ....	195
<i>Kai Larsen</i> : Cytotaxonomical studies in <i>Lotus</i> I. ....	205
<i>Bertil Lindquist</i> : Notes on <i>Cercidiphyllum magnificum</i> Nakai. ....	212
<i>A. Munk</i> : Notes on some Hypocreales recently found in Denmark .....	220
<i>D. Müller</i> : Vorsø set fra luften .....	230
<i>F. H. Møller</i> : The genus <i>Leucopaxillus</i> in Denmark. ....	233
<i>E. Steemann Nielsen</i> : On the preference of some freshwater plants in Finland for brackish water .....	242
<i>R. Nordhagen</i> : Some new observations concerning the geographic distribution and the ecology of <i>Arenaria humifusa</i> in Norway compared with <i>A. norvegica</i> . ....	248
<i>C. Olsen</i> : Hvilke betingelser må være opfyldt for at <i>Helodea canadensis</i> kan opnå den optimale udvikling .....	263
<i>Hugo Osvald</i> : Sloping mires in north-western Norway .....	274
<i>J. Boye Petersen &amp; J. B. Hansen</i> : Electron microscope observations on <i>Codonosiga</i> <i>botrytis</i> .....	281
<i>A. E. Porsild</i> : The North American races of <i>Saxifraga flagellaris</i> Willd. ....	292
<i>K. Rahn</i> : Experimental and cytological studies in <i>Plantago media</i> .....	300
<i>E. Schiemann</i> : Die Geschichte der Kulturpflanzen im Wandel der biologischen Methoden .....	308
<i>C. Skottsberg</i> : Antarctic flowering plants .....	330
<i>Th. Sørensen</i> : Adaptation of small plants to deficient nutrition and a short growing season	339
<i>D. A. Webb</i> : Is the classification of plant communities either possible or desirable...	362
<i>K. Wiinstedt</i> : Nogle indslæbte planter i Pedersborg ved Sorø .....	371

Redaktion: *Morten Lange*.

Færdig fra trykkeriet 18. november 1954.